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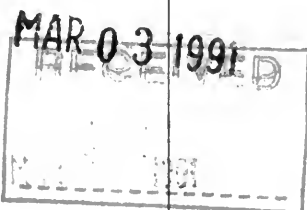
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A MULTIVARIATE STUDY OF THE FAMILY MOLOSSIDAE (MAMMALIA, CHIROPTERA): MORPHOLOGY, ECOLOGY, EVOLUTION

PATRICIA WARING FREEMAN

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This study was originally done in partial fulfillment of the requirements for the degree of Doctor of Philosophy in biology in the graduate school of the University of New Mexico in May, 1977. In the present publication certain sections have been revised and a synonymy and key to the genera have been added as appendices.

The following institutions and their curators kindly supplied me with specimens:

| | |
|------|---|
| AMNH | The American Museum of Natural History, Karl F. Koopman, Curator |
| BJH | Private collection of Bruce J. Hayward, Department of Biology, Western New Mexico University |
| BM | British Museum (Natural History), John E. Hill, Curator |
| FMNH | Field Museum of Natural History, Luis de la Torre, Curator |
| LSU | Louisiana State University Museum of Zoology, the late George H. Lowery, Curator |
| ROM | Royal Ontario Museum, Randolph L. Peterson, Curator; and Judith L. Eger, Curatorial Assistant |
| TCWC | Texas Co-operative Wildlife Collection, Texas A&M University, David Schmidly, Curator |
| UA | University of Arizona, G. Lendell Cockrum, Curator |

- MSB Museum of Southwestern Biology, University of New Mexico,
James S. Findley, Curator
- USNM United States National Museum, Charles O. Handley, Curator; and
Don E. Wilson, Chief, Section of Mammals, National Fish and
Wildlife Laboratories
- WNMU Western New Mexico University, Bruce J. Hayward, Curator

INTRODUCTION

Bats of the family Molossidae are as distinctive as they are elusive. Free-tailed bats are thought to be the swiftest of all bats and tend to fly well above the canopy and out of human reach. Because of such habits, specimens of some species of molossids are not abundant and taxonomic and ecologic knowledge of the family is not extensive.

Molossids are distinctive not only because of their vespertilionoid shoulder, which is at its highest development, narrow wing, and tail, which extends well beyond the posterior border of the uropatagium; but also because of their unique faces, their short, velvety fur, and their tough, leathery skin (Vaughan, 1972, pp. 111-113).

The first molossid to receive a scientific name was *Vespertilio Molossus* Pallas, 1766, from the New World, and so named because of its resemblance to a black mastiff from the Greek province of Molossis. This dog-faced appearance is common to several genera within the family. Actually, *Vespertilio Molossus* included specimens that are now called *Tadarida macrotis* and *Molossus molossus* (Husson, 1962). Many members of the family have deeply wrinkled lips and large ears that project anteriorly and laterally to look like a wide-brimmed hat; others have widely separated, smaller, and more pointed ears and no wrinkles on the lips. Most of the species have unusual spoon-shaped hairs on the muzzle and toes, as well as a gland on the chest which emits an odor unique to molossids.

Molossids are insectivorous and live in tropical and temperate parts of the world. More than half the species are members of the genus *Tadarida*, which historically includes four subgenera: *Chaerephon*, *Mops*, *Mormopterus*, and *Tadarida*. The remaining species are spread among 11 other genera. Species of *Tadarida* (*sensu lato*) are found in both hemispheres, but each region has its own endemic molossid genera: *Molossus*, *Eumops*, *Promops*, *Cynomops*, *Molossops*, and *Neoplatymops* in the New World; and *Otomops*, *Myopterus*, *Platymops*, *Sauromys*, and *Cheiromeles* in the Old World.

The purpose of my study is to examine as many species of the family Molossidae as possible and to determine, with the aid of numerical methods, what natural groups exist within the family. Sneath & Sokal (1973) discuss the methods and reasons for this kind of analysis. A natural group of organisms as here defined is one in which its members share a close phenetic relationship. Phenetic relationship is defined as "similarity (resemblance) based on a set of phenotypic characteristics of the objects or organisms under study," (Sneath & Sokal, 1973, p. 29), and is distinct in definition from phylogenetic relationship. However, I have used phenetic relationships to help estimate phylogenetic ones. I think that the estimation of the evolutionary relationships from phenetics is best observed when size of the organism is not a factor, and for this reason, I place much emphasis on the shape analyses in my study (for a discus-

sion, see Sneath & Sokal, 1973, pp. 168–178). Analysis with size included can be very important in the estimation of ecological relationships.

A natural group of bats in the family Molossidae includes individuals of a certain shape category and can be distinguished from individuals of a different shape category. I think each shape category or group indicates a certain way of life. Often, these natural shape groups correspond with classical genera or subgenera and are described in terms of those taxonomic names. Here, I examine the family Molossidae phenetically, determine how many natural shape groups have evolved within it, predict the resulting diverse ways of life, and estimate the evolutionary relationships among the species and groups. A few of the characters can be graded as to their primitive-derived nature and accompany the evolution discussion. The analyses used were designed not so much to distinguish one species from another, but to detect underlying morphological trends.

No intensive world-wide study of molossids has been attempted. Miller (1907) reviewed the nominal genera known at the beginning of this century and provided morphological descriptions which are precise and meticulous. Early reviews of genera are by Miller (1913) of *Molossus*, by Shamel (1931) of New World *Tadarida*, and by Sanborn (1932) of *Eumops*. All three studies were done with far less material than is available today. Recently, Eger (1977) has examined more closely the genus *Eumops* and rigorously defined the species in that genus.

Prominent taxonomic studies of molossids in the Old World are those by Hill (1961) of Indo-Australian *Tadarida* (*sensu lato*) and by Hayman & Hill (1971). The latter authors offer keys and compilations of information on all African Chiroptera. Koopman (1975) has reviewed the bats of the Sudan and provided much data about Old World Molossids.

Important systematic papers on individual species of molossids are by Peterson (1965, 1967, 1969, 1971a,b, 1972, 1974), who has not only examined many specimens in museums, but has also spent much time in the field collecting the bats and gathering data on their habits and habitat. Recently, Koopman (1978) has added significant zoogeographic and systematic notes on Peruvian molossids. Vaughan (1959, 1966) has studied the wing musculature and flight characteristics of some molossids, and Pye (1966) and Simmons et al. (1978) have done much to reveal the echolocating abilities in molossids.

The following outline is the current status of species of Molossidae examined in this study (for details see Appendix B):

Tadarida Rafinesque, 1814
 (*Tadarida*) Rafinesque, 1814
aegyptiaca E. Geoffroy, 1818
africana Dobson, 1876
ansorgei Thomas, 1913
aurispinosa Peale, 1848
australis Gray, 1838
brasiliensis I. Geof. St. Hilaire, 1824
femorosacca Merriam, 1889
fulminans Thomas, 1903
kuboriensis McKean & Calaby, 1968
laticaudata Geoffroy, 1835
lobata Thomas, 1891

macrotis Gray, 1839
teniotis Rafinesque, 1814
Tadarida
 (*Chaerephon*) Dobson, 1874
aloysiisabaudiae Festa, 1907
bemmelini Jentink, 1879
bivittata Heuglin, 1861
chapini J. A. Allen, 1917
jobensis Miller, 1902
johorensis Dobson, 1873
major Trouessart, 1887
nigeriae Thomas, 1913
plicata Buchanan, 1800

- pumila* Cretzschmar, 1826
russata J. A. Allen, 1917
- Tadarida*
 (Mops) Lesson, 1842
brachyptera Peters, 1852
condylura A. Smith, 1833
congica J. A. Allen, 1917
demonstrator Thomas, 1913
leonis Thomas, 1908
midas Sundevall, 1843
mops de Blainville, 1840
nanula J. A. Allen, 1917
niangarae J. A. Allen, 1917
niveiventer Cabrera & Ruxton, 1926
sarasinorum Meyer, 1899
thersites Thomas, 1903
trevori J. A. Allen, 1917
- Xiphonycteris* Dollman, 1911
spurrelli Dollman, 1911
- Tadarida*
 (Mormopterus) Peters, 1865
acetabulosus Herman, 1804
beccarii Peters, 1881
jugularis Peters, 1865
kalinowskii Thomas, 1863
loriae Thomas, 1897
minutus Miller, 1899
norfolkensis Gray, 1839
phrudus Handley, 1956
planiceps Peters, 1866
- Cheiromeles* Horsfield, 1824
parvidens Miller & Hollister, 1921
torquatus Horsfield, 1824
- Cynomops* Thomas, 1920
brachymeles Peters, 1865
greenhalli Goodwin, 1958
planirostris Peters, 1865
- Eumops* Miller, 1906
auripendulus Shaw, 1800
bonariensis Peters, 1874
glaucinus Wagner, 1843
hansae Sanborn, 1932
maurus Thomas, 1901
perotis Schinz, 1821
underwoodi Goodwin, 1940
- Molossops* Peters, 1865
temminckii Peters, 1865
- Molossus* Geoffroy, 1805
ater Geoffroy, 1805
bondae J. A. Allen, 1904
coibensis J. A. Allen, 1904
molossus Pallas, 1766
pretiosus Miller, 1902
sinaloae J. A. Allen, 1906
trinitatus Goodwin, 1959
- Myopterus* E. Geoffroy, 1818
albatus Thomas, 1915
whitleyi Scharff, 1900
- Neoplatymops* Peterson, 1965
mattogrossensis Vieira, 1942
- Otomops* Thomas, 1913
martienseni Matschie, 1897
papuensis Lawrence, 1948
secundus Hayman, 1952
wroughtoni Thomas, 1913
- Platymops* Peters, 1878
setiger Peters, 1878
- Promops* Gervais, 1855
centralis Thomas, 1915
nasutus Spix, 1823
- Sauromys* Roberts, 1917
petrophilus Roberts, 1917

MATERIALS AND METHODS

Specimens Examined

As explained earlier, my object was to find as many morphologically distinct forms of molossid bats as possible. I assumed that distinct forms or morphotypes are represented by species rather than subspecies. Of an estimated 82 nominal species in the family (Koopman, 1970), 78 were included in my study. Species named in the literature and left out because of difficulty in locating or getting to the specimens are *Molossops aequatorianus* Cabrera, 1957; *Myopterus daubentoni* Desmarest, 1820 (*M. albatus*?, see Hill, 1969); *Otomops formosus*, Chasen, 1939; *Tadarida* (*Mormopterus*) *doriae* Andersen (see Hill, 1961); and the recently described *Tadarida* (*Chaerephon*) *gallagheri* Harrison, 1975.

I attempted to procure an adult male and female of each species, but because

many species of molossids are rare in collections, I often could obtain only one sex. Sexual dimorphism is common in the family, with the male usually being larger and having more distinctive features than the female. I performed a preliminary test on 155 bats to see if males and females of the same species could be safely grouped to represent one morphotype and to see if questionable species or subspecies could be grouped to represent one species or OTU (operational taxonomic unit, see Sokal & Sneath, 1963). With few exceptions, males and females of the same species were phenetically closer to each other than they were to any other bat in the study and subsequently were treated together. Because the magnitude of variation between several subspecies of *Molossus molossus* was slight, I did not believe that individual treatment of the subspecies was justified. *Molossus coibensis*, another possible subspecies of *M. molossus*, was phenetically similar to *M. bondae* and was left in the analysis. The three Australian *Tadarida* (*Mormopterus*), *T. (M.) loriae*, *T. (M.) planiceps*, and *T. (M.) norfolkensis*, were also kept because the 155-bat study did not put males and females of the same species together. There are 80 OTU's in the final analysis on which all discussion is based. Two OTU's are representatives from the family Vespertilionidae, added for comparative purposes.

The specimens used and their abbreviations, which appear in the tables and figures, are listed below. Each number represents an OTU.

1. *Tadarida (Tadarida) aegyptiaca aegyptiaca* (T AEGYPA,¹ Tae)
AMNH 81864 ♂—South Africa: Natal; 16 miles NE Port Shepstone
AMNH 217023 ♀—Kenya: Eastern Prov.; Sultan Hamud
Tadarida (Tadarida) aegyptiaca bocagei
*USNM 156339 ♂—South Africa: Transvaal; Potchefstroom
2. *Tadarida (Tadarida) africana* (T AFRICA, Taf)
BJH 3333 ♂—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
BJH 3341 ♀—same as ♂
3. *Tadarida (Tadarida) ansorgei* (T ANSORA, Tan)
AMNH 48902 ♂—Zaire: Faradje
AMNH 48904 ♀—same as ♂
4. *Tadarida (Tadarida) aurispinosa* (T AURISA, Tau)
TCWC 13897 ♂—Mexico: Tamaulipas; 2 miles W El Abra, Cueva del Abra
TCWC 13895 ♀—same as ♂
5. *Tadarida (Tadarida) australis* (T AUSTRAL, Tas)
*AMNH 153414 ?—Australia: Queensland; Birdsville area
AMNH 220157 ♂—West Australia: Elduna R. H.; 29° 5' S, 127° 25' E
AMNH 220156 ♀—same as ♂
6. *Tadarida (Tadarida) brasiliensis* (T BRASIA, Tb)
MSB 13558 ♂—New Mexico: Socorro Co.; 6½ miles W and 2 miles S Socorro
MSB 13557 ♀—same as ♂

¹Each abbreviation (all capital letters) ending with the letter A represents the average of a male and female specimen.

*An asterisk indicates the specimen was not used in the final analysis containing 80 OTU's.

7. *Tadarida (Tadarida) femorosacca* (T FEMORA, Tfe)
MSB 26859 ♂—Mexico: Sonora; one-half mile E cemetery of Alamos
MSB 26860 ♀—same as ♂
8. *Tadarida (Tadarida) fulminans* (T FULMIN, Tfu)
BM 82.3.134 ♂ type—Madagascar: Fianarantsoa; E Betsileo
9. *Tadarida (Tadarida) kuboriensis* (T KUBORI, Tk)
AMNH 157434 ♀—Papua: Mt. Dayman (Maneau Range), N slope
10. *Tadarida (Tadarida) laticaudata laticaudata* (T LATICA, Tla)
AMNH 75526 ♂—Brazil: Roraima; Mt. Roraima, Paulo
AMNH 75527 ♀—same as ♂
Tadarida (Tadarida) laticaudata europs
*AMNH 79514 ♂—Brazil: Rio Negro, Sta. Maria
11. *Tadarida (Tadarida) lobata* (T LOBATA, Tlo)
BM 70.727 ♂—Kenya: Cherangani Hills; Kaibibich; 1° 10' N, 35° 22' E
ROM 68488 ♀—Kenya: Taita Taveta Dist.; 30 km. SE Voi, Maungu Hill
*ROM 68090 ♂—same as ROM ♀
12. *Tadarida (Tadarida) macrotis* (T MACROA, Tm)
MSB 35601 ♂—New Mexico: Los Lunas
MSB 19223 ♀—New Mexico: Hidalgo Co.; dirt tank N NM79; R19W,
T34S, Sec.33
13. *Tadarida (Tadarida) teniotis* (T TENIOA, Tt)
BM 15.10.2.1 ♂—Egypt: Giza; Aburoash
FMNH 79288 ♀—Egypt: Giza; Abu Rawash
14. *Tadarida (Chaerephon) aloysiisabaudiae* (TC ALOYA, TCa)
ROM 59231 ♂—W. Uganda: Budongo Forest
ROM 38380 ♀—W. Uganda: Budongo Forest, near Masindi
15. *Tadarida (Chaerephon) bemmelini* (TC BEMMI, TCbe)
AMNH 83921 ♂—Tanzania: Mawere
16. *Tadarida (Chaerephon) bivittata* (TC BIVIA, TCbi)
BJH 3338 ♂—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
BJH 3337 ♀—same as ♂
17. *Tadarida (Chaerephon) chapini* (TC CHAPI, TCc)
AMNH 48841 ♂ type—Zaire: Faradje
18. *Tadarida (Chaerephon) jobensis* (TC JOBEN, TCjb)
AMNH 107804 ♂—Australia: Queensland; Malbon
19. *Tadarida (Chaerephon) johorensis* (TC JOHOR, TCjh)
BM 73.637 ♀—Malaya: Kelantan; Pulai
20. *Tadarida (Chaerephon) major* (TC MAJOR, TCm)
AMNH 48838 ♀—Zaire: Faradje
21. *Tadarida (Chaerephon) nigeriae nigeriae* (TC NIGEA, TCni)
USNM 420092 ♂—Ghana: Subinja; Broug-Ahato Region, Oerived
Savannah ca. 2 miles E Wenchi; 7° 45' N, 2° 4' W
USNM 421517 ♀—Dahomey: Segbana, Borgou Region; ≈ 10° 56' N,
3° 42' E
Tadarida (Chaerephon) nigeriae spillmani
*AMNH 115944 ♂—Zambia: Balovale
*AMNH 115947 ♀—same as ♂
22. *Tadarida (Chaerephon) plicata* (TC PLICA, TCpl)
AMNH 101610 ♂—Java: Cheribon
AMNH 107955 ♀—Indonesia: Bali; Noesa Penida

23. *Tadarida (Chaerephon) pumila pumila* (TC PUMIA, TCpu)
 BJH 2191 ♂—Kenya: Naivasha; E edge Lake Naivasha
 BJH 2192 ♀—same as ♂
Tadarida (Chaerephon) pumila gambiana
 *USNM 412176 ♀—Ghana: Volta Region; Bator; 6° 5' N, 0° 25' E
Tadarida (Chaerephon) pumila limbata
 *BJH 3551 ♂—Kenya: 2 miles N Kilifi
 *BJH 3545 ♀—same as ♂
Tadarida (Chaerephon) pumila hindei
 *WNMU 373 ♂—Kenya: Donyo Sabuk Mts.; 32 miles E Nairobi
Tadarida (Chaerephon) pumila nigri
 *AMNH 90390 ♂ paratype—Mali: Timbouctou Dist.; Bourem
24. *Tadarida (Chaerephon) russata* (TC RUSSA, TCr)
 AMNH 48920 ♂—Zaire: Medje
 AMNH 48923 ♀—same as ♂
25. *Tadarida (Mops) brachyptera* (TM BRACH, TMb)
 AMNH 233868 ♀—Uganda: Buganda; Sese Is., Bugala
26. *Tadarida (Mops) condylura* (TM CONDA, TMcd)
 BJH 2462 ♂—Kenya: Kilifi Veterinary Station
 USNM 421490 ♀—Dahomey: Ketou, eastern region; 7° 21' N, 2° 37' E
27. *Tadarida (Mops) congica* (TM CONGA, TMcg)
 AMNH 241063 ♂—Cameroun: 25 km. NE Bertoua
 AMNH 48894 ♀—Zaire: Medje
28. *Tadarida (Mops) demonstrator* (TM DEMOA, TMd)
 AMNH 184432 ♂—Sudan: Bahr el Ghazal Prov.; Yirol Dist., Lake Nyibor
 AMNH 184428 ♀—same as ♂
29. *Tadarida (Mops) leonis* (TM LEONA, TMI)
 AMNH 241079 ♂—Cameroun: 30 km. E Nanga-Emboko
 USNM 414252 ♀—Ghana: Western region, 32 miles W Prestea;
 5° 23' N, 2° 28' W
30. *Tadarida (Mops) midas* (TM MIDAA, TMmi)
 AMNH 184388 ♂—Sudan: Bahr-el-Ghazal; Yirol Dist., Lake Nyibor
 BJH 3332 ♀—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
31. *Tadarida (Mops) mops* (TM MOPSA, TMmo)
 AMNH 234212 ♂—Malaya: Selangor; Fraser's Hill
 BM 19.8.20.2 ♀—Malaya: Selangor; Kuala Lumpur
32. *Tadarida (Mops) nanula* (TM NANUA, TMna)
 AMNH 48863 ♂—Zaire: Niangara
 BJH 3327 ♀—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
33. *Tadarida (Mops) niangarae* (TM NIANG, TMng)
 AMNH 48901 ♂ type—Zaire: Niangara
34. *Tadarida (Mops) niveiventer* (TM NIVEI, TMni)
 AMNH 85525 ♂—Angola: Chitau
35. *Tadarida (Mops) sarasinorum sarasinorum* (TM SARSA, TMs)
 AMNH 109078 ♂—Celebes: Peleng Is.
 AMNH 109063 ♀—same as ♂
Tadarida (Mops) sarasinorum lanei
 *AMNH 241951 ♂—Philippine Is.: Mindanao; Cotabato, Saub
 *AMNH 241990 ♀—same as ♂

36. *Tadarida (Mops) trevori* (TM TREVO, TMtr) -
AMNH 49250 ♀ type—Zaire: Faradje
37. *Tadarida (Mops) thersites* (TM THERA, TMth)
USNM 25208 ♂—Equatorial Guinea: Moka
USNM 25210 ♀—same as ♂
38. *Xiphonycteris spurrelli* (XIPHONYC, X)
USNM 395721 ♂—Equatorial Guinea: Moka
39. *Tadarida (Mormopterus) acetabulosus* (TR ACETA, TRa)
BM 99.11.27.1 ♂—Mauritius
BM 6.11.1.9 ♀—Southern Ethiopia
40. *Tadarida (Mormopterus) beccarii* (TR BECCR, TRb)
AMNH 159401 ♂—Papua: Fergusson Is.; Mapamoiwa
41. *Tadarida (Mormopterus) jugularis* (TR JUGUA, TRj)
USNM 328773 ♂—Madagascar: Tulear Prov.; Tsihombe
USNM 328774 ♀—same as ♂
42. *Tadarida (Mormopterus) kalinowskii* (TR KALIN, TRk)
AMNH 165625 ♂—Peru: Libertad; Trujillo
43. *Tadarida (Mormopterus) loriae* (TR LORIA, TRl)
AMNH 194196 ♂—Australia: N Queensland; Cape York, China Camp
AMNH 154744 ♀—Australia: N Queensland; Cape York, Helenvale, 20
miles S Cooktown
44. *Tadarida (Mormopterus) minutus* (TR MINUA, TRm)
AMNH 4195 ♂ type—Cuba: Trinidad
AMNH 4914 ♀—same as ♂
45. *Tadarida (Mormopterus) norfolkensis* (TR NORFA, TRn)
AMNH 154735 ♂—Australia: Cape York; Mossman
AMNH 154737 ♀—Australia: Cape York; Cairns
46. *Tadarida (Mormopterus) phrudus* (TR PHRUD, TRph)
AMNH 91553 ♂—Peru: Machu Picchu
47. *Tadarida (Mormopterus) planiceps* (TR PLANA, TRpl)
AMNH 220093 ♂—Australia: Victoria; Carisbrook
AMNH 220094 ♀—Australia: Victoria; 18 miles NW Underbool
48. *Cheiromeles parvidens* (C PARVID, Cp)
AMNH 241942 ♂—Philippine Is.: Mindanao; Cotabato, Saub
49. *Cheiromeles torquatus* (C TORQUT, Ct)
ROM 44147² ♀—Philippine Is.: Negros Is.
*AMNH 103922 ♀—Borneo (NE): Peleben
50. *Cynomops brachymeles* (CP BRACA, CPb)
AMNH 239235 ♂—Paraguay: Guaira; Villarrica
AMNH 23800 ♀—Paraguay: Sopucay
51. *Cynomops greenhalli* (CP GREEA, CPg)
AMNH 183868 ♂—Panama: Canal Zone; Cocoli
AMNH 176285 ♀—Trinidad: Port of Spain; Botanic Gardens
52. *Cynomops planirostris* (CP PLANA, CPp)
AMNH 234457 ♂—Paraguay: Dept. Olimpo; Fuerte Olimpo
AMNH 17096 ♀—Venezuela: Maripa

²It came to my attention only after my study was completed that this specimen may not be true *torquatus*.

53. *Eumops auripendulus* (E AURIPA, Ea)
AMNH 93851 ♂—Brazil: Rio Amazon, N bank; Faro
AMNH 93855 ♀—same as ♂
54. *Eumops bonariensis* (E BONARA, Eb)
AMNH 205653 ♂—Uruguay: Dept. Rio Negro; Arroyo Negro, 15 km S Paysandu
AMNH 205661 ♀—same as ♂
55. *Eumops glaucinus* (E GLAUCA, Eg)
AMNH 207926 ♂—Colombia: Dept. Cundinamarca; Bogota
AMNH 130700 ♀—Venezuela: Rio Tocuyo
56. *Eumops hansae* (E HANSAA, Eh)
LSU 11487 ♂—Costa Rica: Puntarenas; 10 miles S Palmar Sur
USNM 310278 ♀—Panama: Darien; Tacarcuna
57. *Eumops maurus* (E MAURUS, Em)
BM 1.6.4.34 ♂ type—Guiana: Kanuku Mts.
58. *Eumops perotis perotis* (E PEROTA, Ep)
MSB 4300 ♂—Arizona: Pima Co.; Tucson
MSB 31266 ♀—New Mexico: Hidalgo Co.; 32 miles S Rodeo
*AMNH 185208 ♂—Argentina: Yuto; Jujuy
Eumops perotis trumbulli
*AMNH 97016 ♂—Brazil: R. Tocantins; Mocajuba
*AMNH 97022 ♀—same as ♂
59. *Eumops underwoodi* (E UNDERA, Eu)
UA 8112 ♂—Arizona: Pima Co.; ca. 10 miles NNW Sasabe, Encinas Wash, Baboquivari Mt., T21S, R7E
MSB 10697 ♀—Arizona: Pima Co.; Garcia Represso, 2 miles E Sasabe
60. *Molossops temminckii* (MP TEMMA, MP)
AMNH 186950 ♂—Argentina: Yuto; Jujuy
AMNH 181537 ♀—same as ♂
61. *Molossus ater* (M ATERA, Ma)
AMNH 183317 ♂—Colombia: Norte de Santander; Cucuta
MSB 31532 ♀—Mexico: Sinaloa; Rio Magistral, 8.4 miles E Concordia on Hwy. 40
62. *Molossus bondae* (M BONDAA, Mb)
AMNH 212908 ♂—Panama: Canal Zone; Ft. Sherman, 5 km. W Colon
AMNH 183322 ♀—Colombia: Norte de Santander; Cucuta
63. *Molossus coibensis* (M COIBEA, Mc)
MSB 27876 ♂—Panama: Canal Zone; Barro Colorado Is.
MSB 29170 ♀—same as ♂
64. *Molossus molossus molossus* (M MOLOSS, Mm)
AMNH 212295 ♂—Colombia: Dept. Cundinamarca; Sasaima
Molossus molossus barnesi
*BM 5.1.8.7 ♀ type—French Guiana: Cayenne
Molossus molossus lambi
*AMNH 217440 ♂—Guatemala: Dept. Jutiapa; Col Montufar, ca. 12 miles S Pedro Alvarado
Molossus molossus pygmaeus
*AMNH 30393 ♂ topotype—Netherlands West Indies: Curacao

65. *Molossus pretiosus* (M PRETIA, Mp)
AMNH 23780 ♂—Venezuela: La Guaira
AMNH 23781 ♀—same as ♂
66. *Molossus sinaloae* (M SINALA, Ms)
AMNH 204985 ♂—Yucatan: Cenote, 2 km. N Hunucma
AMNH 41190 ♀—Nicaragua: Sioux Plantation, 125 miles up Rio Grande, Sixicuas Creek
67. *Molossus trinitatus* (M TRINIA, Mt)
AMNH 179987 ♂ type—Trinidad: Port of Spain; Belmont
AMNH 7521 ?—Trinidad: Port of Spain
68. *Myopterus albatrus* (MYOP ALB, MYa)
AMNH 48855 ♀—Zaire: Niangara
69. *Myopterus whitleyi* (MYOP WHA, MYw)
BM 26.7.6.99 ♂—Zaire: Kasai; Luluabourg
BM 26.11.1.46 ♀—Zaire: Kasai; Luluabourg
70. *Neoplatymops mattogrossensis* (NEOPLATA, N)
AMNH 149150 ♂—Venezuela: Amazonas Terr.; Tapara, upper Rio Cunucunuma NW Cerro Dvida
ROM 32984 ♀—Guiana: Rupununi Dist.; 15 miles E Dadanawa
*ROM 32986 ♂—same as ROM ♀
71. *Otomops martiensseni* (OTO MARA, Om)
AMNH 88115 ♂—Angola: Chitau
BJH 2337 ♀—Kenya: Rift Valley; cave on Mt. Suswa, 35 miles WNW Nairobi
72. *Otomops papuensis* (OTO PAPU, Op)
BM 73.136 ♂—New Guinea: Mt. Suckling; Maul
73. *Otomops secundus* (OTO SECA, Os)
BM 50.982 ♂ type—New Guinea (NE): Upper Ramu River Plateau, Tapu
BM 50.979 ♀—same as ♂
74. *Otomops wroughtoni* (OTO WROA, Ow)
BM 13.4.9.3 ♂—India: Talawadi; Parapede Cave
BM 13.4.9.6 ♀—same as ♂
75. *Platymops setiger* (PLATYMOA, P)
BJH 2473 ♂—Kenya: 10 miles N Kiboko, ca. 100 miles SE Nairobi
AMNH 219867 ♀—Kenya: Rift Valley; Lake Baringo, Kampi ya Samaki
76. *Promops centralis* (PRO CENA, PRc)
AMNH 126828 ♂—Honduras: La Paz; Los Encuentros
AMNH 126854 ♀—Honduras: La Paz; El Pedrero
77. *Promops nasutus ancilla* (PRO NASU, PRn)
AMNH 184647 ♀—Argentina: Jujuy; Yuto
Promops davisoni
*AMNH 34382 ?—Ecuador: Manavi, Rio de Oro
*LSU 16639 ♀—Peru: Dept. Lima; Canete
78. *Sauromys petrophilus* (SAUROMYS, S)
AMNH 165942 ♂—Botswana: Molepolole
79. *Vespertilionidae*—*Nyctalus nacula* (NYCTALUS, NY)
AMNH 162809 ♂—Germany: Bavaria; Haag a/Amper

80. Vespertilionidae—*Mimetillus moloneyi* (MIMETILL, MI)

USNM 424872 ♂—Ghana: Volta Region; Leblebi Agbesia, 6° 56' N,
0° 25' E

Characters Used

I employed the exemplar method of Sneath & Sokal (1973, p. 183). Characters in my study included 56 morphometric measurements, 12 qualitative multistate codes, and eight ratios. The morphometric measurements are standard ones from the skull, wings, and body. Codes are features which are hard to measure, but which have been emphasized historically as being important in defining molossid species. Ratios used are those which have been used by other authors, or those which are proportional to a reliable size measurement. It could be argued that characters should be as uncorrelated as possible, but had only uncorrelated characters been used, many fewer measurements would have been taken, and some functionally important trends could have been missed. In addition, I think that maintaining a large number of characters gave rise to a robust arrangement of OTU's in the principal components analysis, so that changes in the number of OTU's or kinds of characters or both had little effect on the representation of the basic morphological relationship among the bats.

A preliminary study of 22 species indicated several characters that could be interpreted ecologically. I derived the final list of characters by removing the ones which could not be accurately measured or quantified and by adding ones which were related to functionally relevant morphological trends indicated by the study of 22 bats. For example, several characters concerned with the jaw were added which would better describe changes in that structure.

The qualitative multistate characters (codes) were the most difficult to handle because quantification involved substantial subjectivity. An overview of the variation among all the bats was attained before reasonable coding could be done. Here, the codes show degrees of change (qualitative multistates) and are made as continuous as possible. I did not include lower incisor number as a character.

Measurements were taken under a dissecting microscope and were carried to the nearest 0.1 mm with Helios dial calipers. For two measurements, width of angular process and height of condyle above the lower toothrow, a cross hair reticle in the microscope was necessary. For many of the dentary measurements, it was more convenient to use articulated mandibles rather than disarticulated ones. The scale in the drawings of the skulls is equal to 1 mm, and all drawings in Figures 9-20 are drawn to scale.

All 76 characters are described in detail below and are illustrated in Figure 1. Abbreviations used in the figures, tables, and text are given for each character.

General body characters

1. Head and body (HB)—length from tag or alcoholic specimen
2. Tail (TAIL)—length from tag or alcoholic specimen
3. Ear (EAR)—length from tag or alcoholic specimen
4. Hindfoot (HF)—length from heel to end of longest toenail on dry or wet specimen
5. Tibia (TIBIA)—length from knee joint at indentation between femur and tibia to distal end of tibia (not including tarsals)

6. Forearm (FA)—length from olecranon process to shallow notch proximal to thumb (including carpals)
7. Third metacarpal (3 META)—length from distal endpoint for FA to distal end of bone
8. Third metacarpal first phalanx (3M 1PHAL)—greatest length of bone
9. Third metacarpal second phalanx (3M 2PHAL)—greatest length of bone
10. Third metacarpal third phalanx and tip (3M TIP)—length from proximal end of third phalanx to distal end of cartilaginous tip (curve of tip measured in two straight lines breaking at greatest point in curve)
11. Fourth metacarpal (4 META)—length from distal endpoint for FA to distal process of bone
12. Fourth metacarpal first phalanx (4M 1PHAL)—greatest length of bone
13. Fourth metacarpal second phalanx (4M 2PHAL)—greatest length of bone (no cartilage included)
14. Fifth metacarpal (5 META)—length from distal endpoint for FA to distal process of bone
15. Fifth metacarpal first phalanx (5M 1PHAL)—greatest length of bone
16. Fifth metacarpal second phalanx (5M 2PHAL)—greatest length of bone plus cartilaginous tip
17. Digit three (DIGIT 3)—sum of metacarpal 3, phalanges, and tip
18. Digit four (DIGIT 4)—sum of metacarpal 4 and phalanges
19. Digit five (DIGIT 5)—sum of metacarpal 5, phalanges, and tip

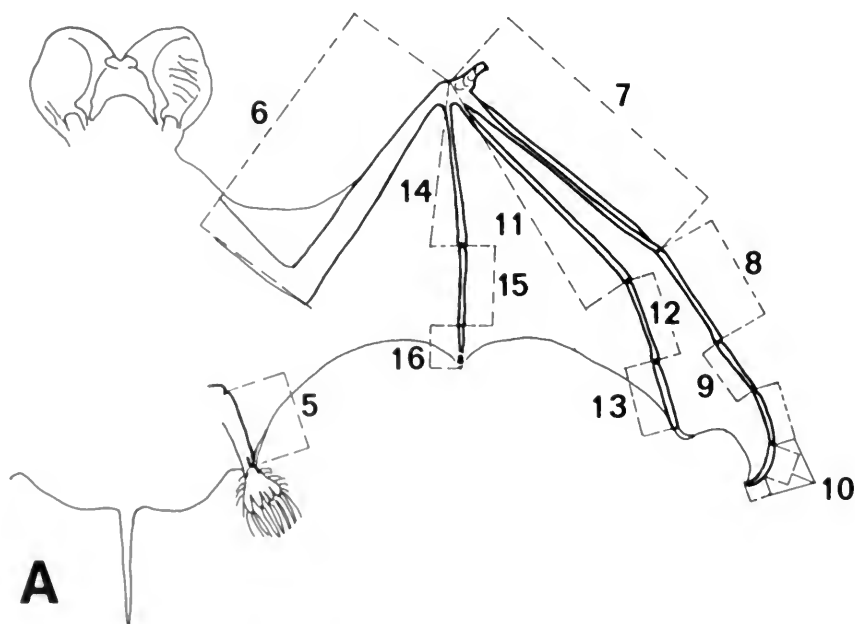


FIG. 1. The limits of each measurement on the wing and body (A) and skull and mandible (B). Numbers correspond with the measurements described in Materials and Methods.

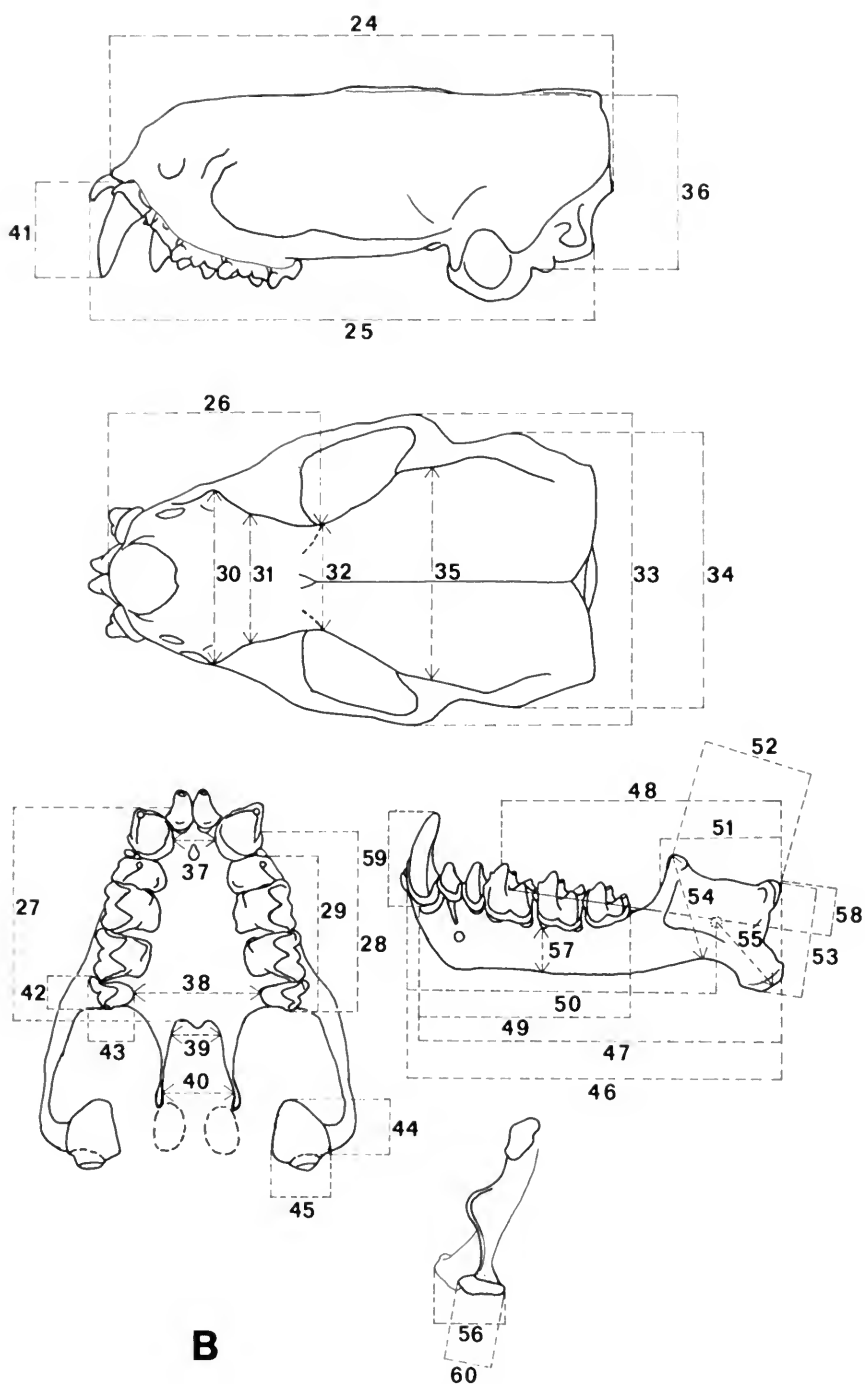


FIGURE 1.

- R20. Aspect ratio (ASPECT)—DIGIT 3 plus FA divided by DIGIT 5
 R21. Tip index (TIP INDX)—DIGIT 3 divided by DIGIT 3 plus FA, times 100
 R22. Digit three divided by digit five (D3 I D5)
 R23. Ear divided by forearm (EAR I FA)

Skull measurements

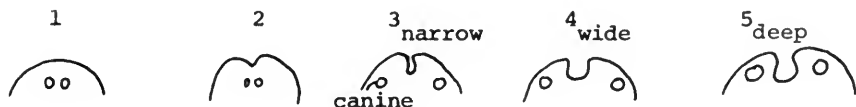
24. Greatest skull length (GSL)—from posteriormost part of occipital to anteriormost point of the premaxillary bone (taken on a line parallel to line connecting foramen magnum and anterior point on the premaxillary)
25. Condylolincisive length (CON INCI)—from occipital condyle to anteriormost point of upper incisors
26. Rostral length (ROST LEN)—from cribiform plate to anteriormost point of premaxillary bone
27. Palatal length (PALATE)—from posterior border of hard palate to anterior border of premaxillary bone
28. Maxillary toothrow (MTR)—length from anterior alveolar border of canine to posterior alveolar border of M³
29. Upper molariform row (UP MOL R)—length from PM⁴ to M³ (alveolar)
30. Lacrimal width (LACR WID)—width across rostrum dorsally at protuberances near lacrimal canals
31. Interorbital width (INTORB W)—width across rostrum dorsally between lacrimals and least constriction
32. Postorbital width (POST ORB)—dorsal width at most constricted part of skull
33. Zygomatic breadth (ZYGO BR)—width taken across zygomatic arches at widest point near posterior junction with braincase
34. Breadth at mastoids (MASTOID)—greatest breadth at mastoid processes
35. Breadth braincase (BR BCASE)—breadth just dorsal to posterior juncture of zygomatic process
36. Height of braincase (BCASE HT)—from basisphenoid and basioccipital bones to top of braincase on either side of sagittal crest
37. Width at upper canines (C1 C1)—width between alveolar borders of upper canines
38. Width at upper molars (M3 M3)—width between alveolar borders of upper third molars
39. Width at anterior pterygoids (ANT PTER)—width at anterior divergence of pterygoid processes
40. Width at posterior pterygoids (POSTPTER)—width at posterior part at middle depth of pterygoid processes
41. Height upper canine (UP CANIN)—greatest length from point immediately dorsal to cingulum to end of tooth (not taken if too worn)
42. Length M³ (M3 LENG)—anterior-posterior length of tooth
43. Width M³ (M3 WIDTH)—greatest lateral-medial width of tooth
44. Length glenoid fossa (GLENO L)—anterior-posterior length of fossa from middle of face of postglenoid process to anteriormost rim of fossa
45. Width glenoid fossa (GLENO W)—greatest lateral-medial width of fossa (light must be good to see fossa rims)

Dentary characters

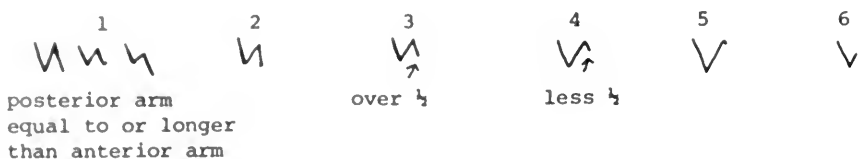
46. Dentary length (DENT LEN)—from midpoint of mandibular condyle to anteriormost point of dentary
47. Condyllocanine length (CON CANI)—from midpoint of condyle to anterior border of alveolus of lower canine
48. Condyle to M₁ (COND M1)—length from midpoint of condyle to anterior face of protoconid on first lower molar
49. Lower tooththrow (LOWER TR)—length from posterior alveolar border of M₃ to anterior alveolar border of C₁
50. Length mandibular foramen to anterior dentary (FOR ANT)—from medial foramen at base of coronoid process to anteriormost point of dentary
51. Condyllo-coronoid length (CON CORO)—from middle of longitudinal axis of condyle to anterior face of coronoid directly opposite
52. Moment arm of temporal (MOM1 COR)—length from middle of condyle to tip of coronoid process
53. Moment arm of masseter (MOM2 ANG)—length from middle of condyle to tip of angular process
54. Height of coronoid (CORO HT)—from indentation of ventral mandibular border to tip of coronoid (easiest to take on articulated mandibles)
55. Length angular process (ANGUL L)—from mandibular foramen to tip of angular
56. Width angular process (ANGUL W)—actually the amount of splaying laterally of the angular. Taken with vertical cross hair of microscope lined up with medial border of condyle and horizontal cross hair at the posterior tips of both angular processes. Calipers are braced on a finger to line up one side with the vertical.
57. Dentary thickness (DENTTHIC)—width of dentary at base of protoconid of M₂ taken on the lateral surface (calipers must be braced)
58. Height of condyle above the tooththrow (TR CON H)—horizontal cross hair in microscope aligned with valleys at the bases of hypoconid and protoconid of M₁ and M₃ (these have less wear than the tops of the cusps). Height taken from this line to top of condyle with braced calipers.
59. Height lower canine (LO CANIN)—greatest length from point immediately ventral to cingulum to top of tooth (not taken if too worn)
60. Length condyle (CONDY L)—medial-lateral length of mandibular condyle
- R61. Condyle height/dentary length (CONHT DL)—TR CON H divided by DL
- R62. Dentary thickness/dentary length (DTHIC DL)—DENTTHIC divided by DL
- R63. Moment arm index (M1+M2 DL)—MOM1 COR (temporal) plus MOM2 ANG (masseter) divided by DL
- R64. Coronoid height/dentary length (COR H DL)—CORO HT divided by DL

Qualitative multistate characters (codes)

- C65. Incisive foramina (INCI FOR)—degree of emargination of anterior palate, states as follow from closed to open:



C66. Shape of cusp on M³ (N SHAPE)—degree of change of cusp pattern on upper third molar, states as follow from N to V shape:



C67. Development of PM³ (PREMOLAR)—degree of development of upper third premolar, states as follow, from absence to presence:

| | | | |
|------|-------------------------|----------|-------|
| 1 | 2 | 3 | 4 |
| none | small (or vestigial) | moderate | large |

C68. Development of metaconule on M¹ (M1 META)—states as follow, from slightly distinct to very distinct:

| | | |
|--------|----------|---------------|
| 1 | 2 | 3 |
| slight | moderate | very distinct |

C69. Development of basisphenoid pits (BASI PIT)—states as follow, from none to very deep:

| | | | | |
|------|---------|----------|------|-----------|
| 1 | 2 | 3 | 4 | 5 |
| none | shallow | moderate | deep | very deep |

C70. Development of anterior sagittal crest (A SAGITT)—states as follow, from slight to great:

| | | |
|-------------------|----------|-------|
| 1 | 2 | 3 |
| none or slight | moderate | great |

C71. Development of posterior sagittal crest (P SAGITT)—states as follow, from slight to great:

| | | |
|-------------------|----------|-------|
| 1 | 2 | 3 |
| none or slight | moderate | great |

C72. Development of lateral lambdoidal crest (L LAMBDO)—states as follow, from slight to great:

| | | |
|-------------------|----------|-------|
| 1 | 2 | 3 |
| none or slight | moderate | great |

C73. Development of superior lambdoidal crest (S LAMBDO)—states as follow, from slight to great:

| | | |
|-------------------|----------|-------|
| 1 | 2 | 3 |
| none or slight | moderate | great |

C74. Quality of ear junction (EAR JUNC)—states as follow, from well separated to well joined above the nose

| 1 | 2 | 3 |
|----------------|---|------------------------------------|
| well separated | V-shaped valley, not joined or only just joining at bases | well joined over nose with band |

C75. Quantity of spoon hairs or spines on lips (HAIRYNES)—states as follow, from none to many:

| 1 | 2 | 3 |
|------|-----|------|
| none | few | many |

C76. Degree of wrinkling on the upper lip (WRINKLES)—states as follow, from none to finely wrinkled:

| 1 | 2 | 3 | 4 |
|------|----------------------|-----------------------|---|
| none | few (less than 7) | many (more than 7) | many fine microscopic wrinkles (lips are skirt-like) |

Statistical Analyses

The analyses used are from the packaged Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) developed by Rohlf et al. (1974). Data were standardized and analyzed by the following: principal components analysis or principal coordinates analysis (PCA), correlation, distance and reduced distance (Gower transformation), and phenograms by the unweighted pair-group method using arithmetic averages (UPMGA). All computer work was done on an IBM 360 model computer housed at the University of New Mexico Computer Center. A summary program, developed by G. Michael Schum at the University of New Mexico, producing all coefficients of variation, maximum and minimum distances of each OTU, and highest and least correlations of each OTU, was also employed. Good explanations of all the multivariate analyses used in this study can be found in Sneath & Sokal (1973).

Several major variations of the data were run and are listed as follows:

- 22 OTU's and 60 characters as a preliminary study
- 36 OTU's and 78 characters (raw measurements expressed as ratios)
- 155 OTU's and 65 characters (raw + codes) as a grouping study
- 80 OTU's and 53 characters (raw)
- 80 OTU's and 65 characters (raw + codes)
- 80 OTU's and 64 characters (raw + ratios)
- 80 OTU's and 76 characters (raw + codes + ratios)

All descriptions are based on the analysis with 80 OTU's, including 78 molossid species and two vespertilionid species; and 76 characters including 56 raw measurements, eight ratios, and 12 codes. The principal components analysis (PCA) proved to be a robust technique, because changing the number of OTU's or type of characters or both had little effect on the representation of the basic pattern of OTU's on the first few principal components.

I used several techniques for analysis because one alone does not adequately represent the multivariate data. The principal components analysis is an ordination technique and reveals clusters of phenetically similar bats. The distance

and correlation analyses are clustering techniques and detect nearest neighbor relationships.

In my principal components analysis, component I is a size component as it is in many biological studies where many size-related morphological features were measured. This first component accounts for 60 per cent of the total variation in the data. The second, third, and fourth components account for 12, 6, and 3 per cent of the variation, respectively. These components are shape-related. Because size does account for so much of the variation in the data and thus may obscure other trends, I think it is desirable to look only at the shape-related components to see how phenetically similar the bats are, whether large or small. I think shape-related morphology is more important in determining the phenetic and evolutionary relationships among the bats, whereas the size-related morphology is more important in determining the ecological relationships among the bats. Consequently, the first component can be eliminated when necessary, and only the second, third, and fourth components studied. This procedure, called "size-out," essentially subtracts the contribution of the first component from the distances among the OTU's (see Sneath & Sokal, 1973, pp. 172-173, for details). The size-out PCA is very similar to an earlier PCA done on all ratio data. I use size-out extensively for the morphological descriptions of the groups and in the examination of the evolutionary relationships. I use combined size and shape components (size-in) to support the morphological description, but primarily to analyze faunal composition.

Other Methods

The analysis of fecal samples that I used is one modified after Black (1974). I stained the fecal material with eosine, let it dry, put a portion on a slide, and weighed the exact amount with an analytical balance. I covered the weighed portion with Per-Mount and coverslip and let it dry. I took three different counts of moth scales in a 10- by 10-mm grid in a Wild M5 dissecting microscope and made an average for the sample. The result was an estimated count of scales per gram of fecal material.

GENERAL DESCRIPTION OF THE PRINCIPAL COMPONENTS

Because the first component is highly correlated with size, nearly all of the raw measurements are highly positively correlated with this axis. The largest bats are on the far positive end, and the smallest, on the negative end (fig. 2). As an example of the sizes involved, *Cheiromeles parvidens* has a GSL^3 of 30 mm, whereas *Tadarida (Mormopterus) minutus* has a GSL of 13 mm (table 1, appendix A). A frequency distribution of GSL 's shows this measurement to be distributed log normally and to correspond well with the frequency distribution of OTU's on the first principal component (fig. 3).

Highly correlated with the second principal component are characters related to the shape of the jaw and teeth. The highest character loadings on all components are listed in Table 2. The second component or axis can be viewed in

³The GSL is used as a measure of size in the molossids because weights, probably the best measure, were not always available. Forearm length does not always correspond to general body size (Verschuren, 1957), and head and body length from the tag is un dependable.

TABLE 1. Greatest skull lengths of molossid bats ordered from smallest to largest (*Sauromys* and *Platymops* are listed under *Mormopterus*; *Molossops*, *Neoplatymops*, *Cynomops*, *Myopterus*, and *Cheiromeles*, under Conglomerate; and *Promops*, under *Otomops*).

| Size (mm.) | <u>Tadarida</u> | <u>Chaerephon</u> | <u>Mops</u> | <u>Mormopterus</u> | Conglomerate | <u>Eumops</u> | <u>Molossus</u> | <u>Otomops</u> |
|---------------|----------------------|----------------------------------|----------------------|--|----------------------|----------------------|----------------------|----------------|
| 13.0- 13.9 | | | | TR MINUA | MP TENMA NEOPLATA | | | |
| 14.0 | | | XIPHONYC | TR ACETA TR LORIA | | | | |
| 15.0 | | | TM NANUA | TR MORFA TR KALIN TR PLANA TR PHRUD PLATYMOP | CP PLANA | | N COIBEIA | |
| 16.0 | T SRASIA | TC CHAPI | | TR JUGUA | | | | |
| 17.0 | | TC MAJOR TC PUMIA TC BENMI | TM LEONA | SAUROMYS | CP GREEA MYOP WHA | | N MOLOSS N BONDAA | PRO NASU |
| 18.0 | T LATICA T ANSORA | TC RUSSA TC NIGEA | TM BRACH TM TMERA | TR BECCR | | | N TRINIT | |
| 19.0 | T FEMORA T AEGYPA | TC JOHOR TC PLICA TC BIVIA | TM SARSA | | | E HANSAA E BONARA | N GINALA | OTO PAPU |
| 20.0 | T AURISA | | TM DEMOA TM CONDA | | CP BRACA | E MAURUS | N PRETIA | PRO CENA |
| 21.0 | T KUBORI | TC ALOYA TC JOBEN | TM NIVEI TM MOPSA | | | | N ATERA | OTO SECA |
| 22.0 | T FULMIN T LOBATA | | | | | | | |
| 23.0 | T MACROA T AUSTRA | | TM NIANG TM TREVO | | MYOP ALB | E GLAUCA E AURIPA | | |
| 24.0 | T TENIOA T AFRICA | | | | | | | OTO WROA |
| 25.0 | | | TM CONGA | | | | | |
| 26.0 | | | | | | | | |
| 27.0 | | | TM MIDAA | | | E UNDERA | | OTO MARA |
| 28.0 | | | | | | | | |
| 29.0 | | | | | C TORQUT | | | |
| 30.0 | | | | | C PARVID | E PEROTA | | |

several plots: with component I in Figure 2A and with components III and IV in Figure 4. In all figures, the relative thickness of the dentary is greater in bats on the positive end as are three other characters related to the jaw: relative sum of muscle moment arms, relative height of coronoid process, and relative height of mandibular condyle above the toothrow. Bats on the positive end also have V-shaped (and shorter) M^3 's and little or no development of PM^3 . Development of sagittal and lambdoidal crests is greater in bats on the positive end, and the number of spoon hairs or spines around the mouth is higher in bats on the positive end, but they have shorter ears and no palatal emargination.

In contrast, bats on the negative end of axis II have the following morphological features: thin jaws, condyles in line with the toothrow, low coronoid processes, N-shaped (longer) M^3 's, well-developed PM^3 's, undeveloped cranial crests, a lesser degree of hairiness, longer ears, and a wide palatal emargination. Illustrative extremes on axis II are *Cheiromeles* and *Molossus* on the positive, thick-jawed end, and *Otomops* and *Tadarida macrotis* on the negative, thin-jawed end.

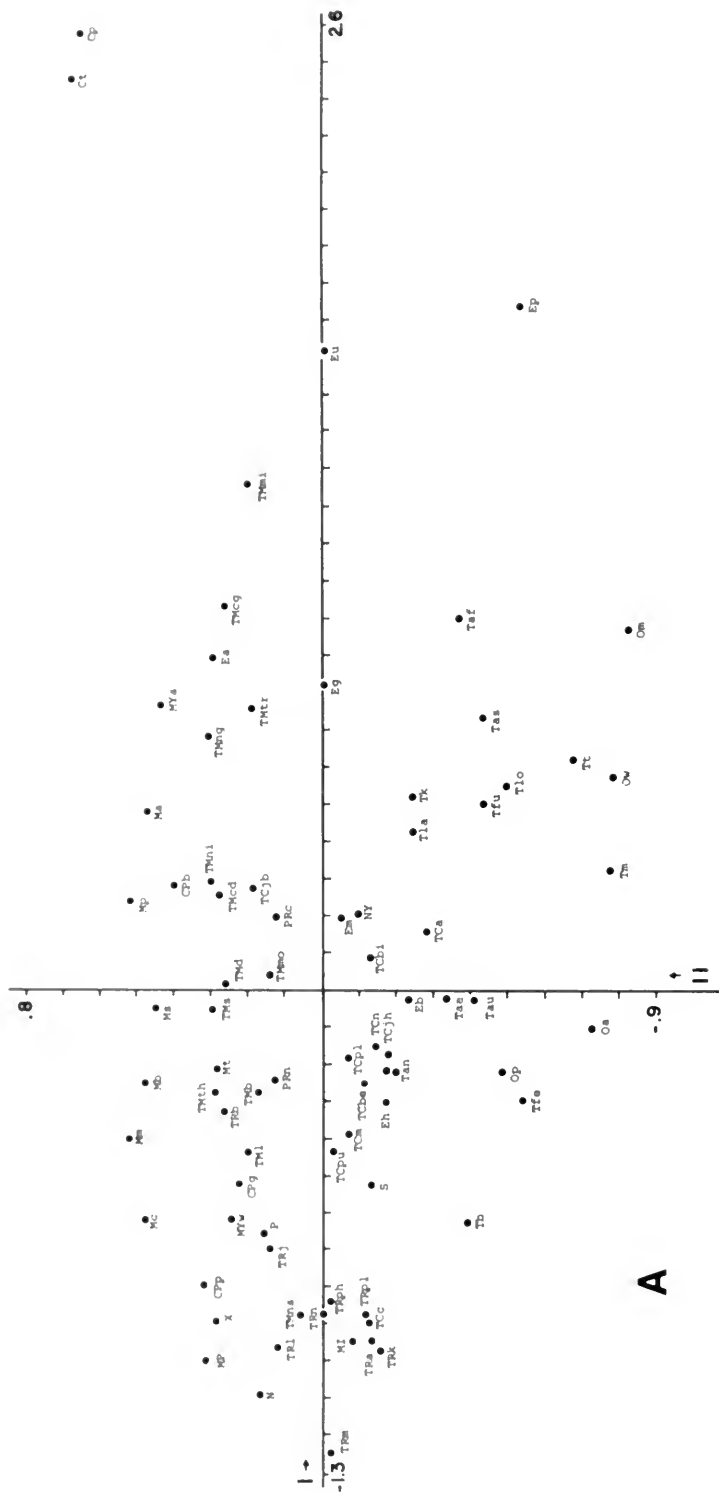


FIGURE 2.

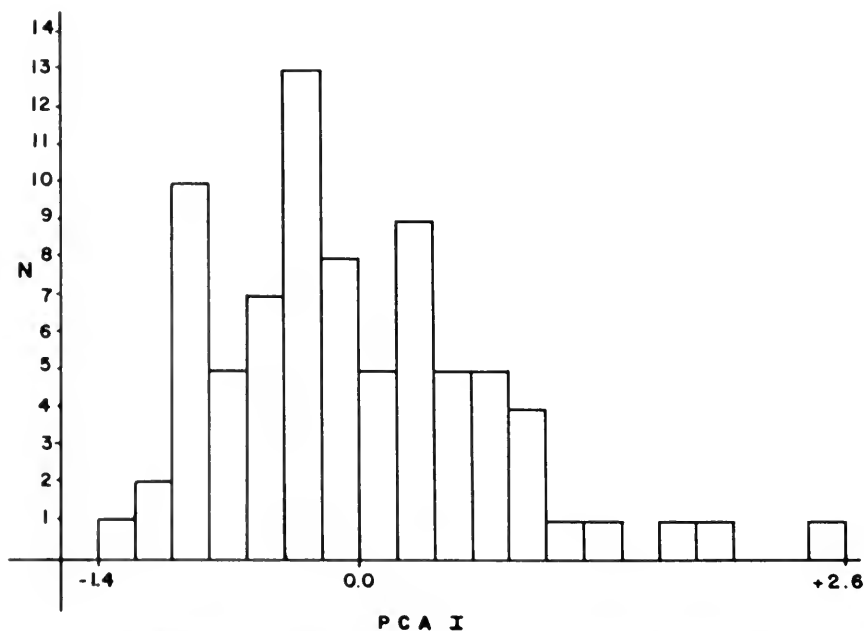
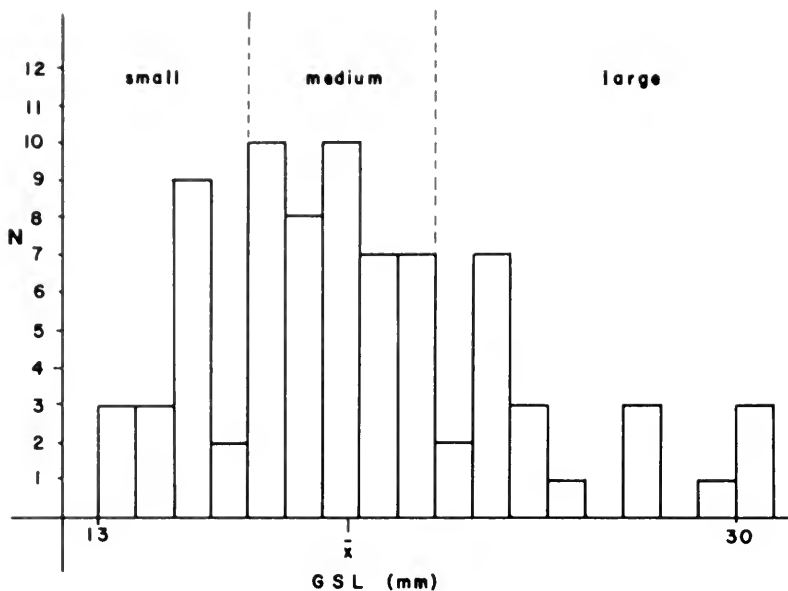


FIG. 3. Comparison of frequency distributions of the character, greatest skull length, and principal component I. The dashed lines delineate small, medium, and large bats and are drawn at approximately one-half standard deviation units from the mean.

TABLE 2. Twenty most highly correlated characters for each of the first four principal components and percentage of the total variation accounted for by each factor.

| | Component I | Component II | Component III | Component IV |
|---------------|----------------|----------------|----------------|----------------|
| Character | DENT LEN .984 | DTHIC DL .855 | EAR JUNC -.701 | L LAMBDO .733 |
| Correlations | CON CANI .984 | M1+M2 DL .839 | A SAGITT -.688 | 4M 2PHAL -.595 |
| | COND M1 .981 | COR H DL .749 | BASI PIT -.552 | EAR JUNC -.467 |
| | UP MOL R .977 | N SHAPE .720 | COR H DL .543 | EAR I FA -.447 |
| | GSL .976 | CONHT DL .707 | INTORB W .488 | PREMOLAR -.400 |
| | LOWER TR .974 | PREMOLAR -.690 | INCI FOR .453 | 3M TIP -.360 |
| | ZYGO BR .974 | TR CON H .646 | N SHAPE -.424 | TAIL .350 |
| | HEAD BOD .971 | P SAGITT .638 | ANGUL W -.412 | C1 C1 -.325 |
| | CON INCI .970 | S LAMBDO .636 | LACR WID .409 | S LAMBDO -.322 |
| | MTR .964 | HAIRYNES .600 | C1 C1 .394 | INCI FOR -.263 |
| | DIGIT 3 .963 | M3 LENG -.588 | CONHT DL .391 | CONHT DL -.255 |
| | DIGIT 4 .960 | WRINKLES -.553 | TR CON H .387 | D3 I D5 -.250 |
| | MOM1 COR .959 | EAR -.549 | CORO HT .377 | HAIRYNES -.234 |
| | BCASE BR .955 | EAR I FA -.523 | HAIRYNES -.362 | TR CON H -.232 |
| 3M 2PHAL .953 | INCI FOR -.510 | POST ORB .349 | 5M 2PTIP .227 | |
| CON CORO .952 | DENTHTIC .469 | D3 I D5 -.327 | ASPECT -.224 | |
| MASTOIDB .950 | CORO HT .450 | S LAMBDO -.317 | 4M 1PHAL .186 | |
| 3M 1PHAL .943 | M1 META -.438 | 4M 2PHAL .291 | 5 META .172 | |
| PALATE L .941 | TIP INDX .435 | M3 LENG .281 | P SAGITT .169 | |
| GLENO W .941 | ANGUL W .393 | P SAGITT -.276 | M3 WIDTH .166 | |
| % variation | 60.29 | 12.16 | 6.16 | 3.74 |
| % accumulated | 60.29 | 72.44 | 78.60 | 82.35 |

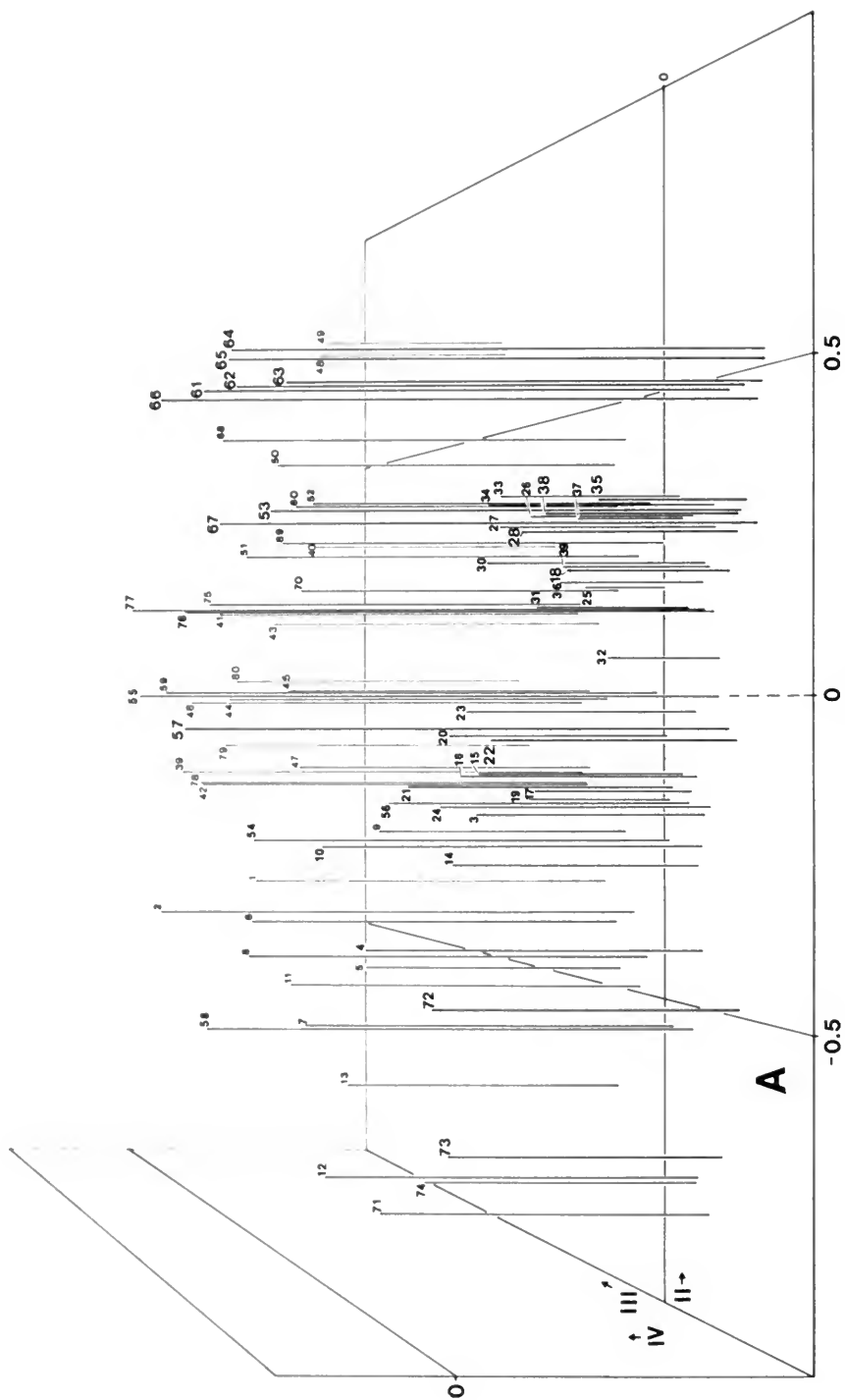
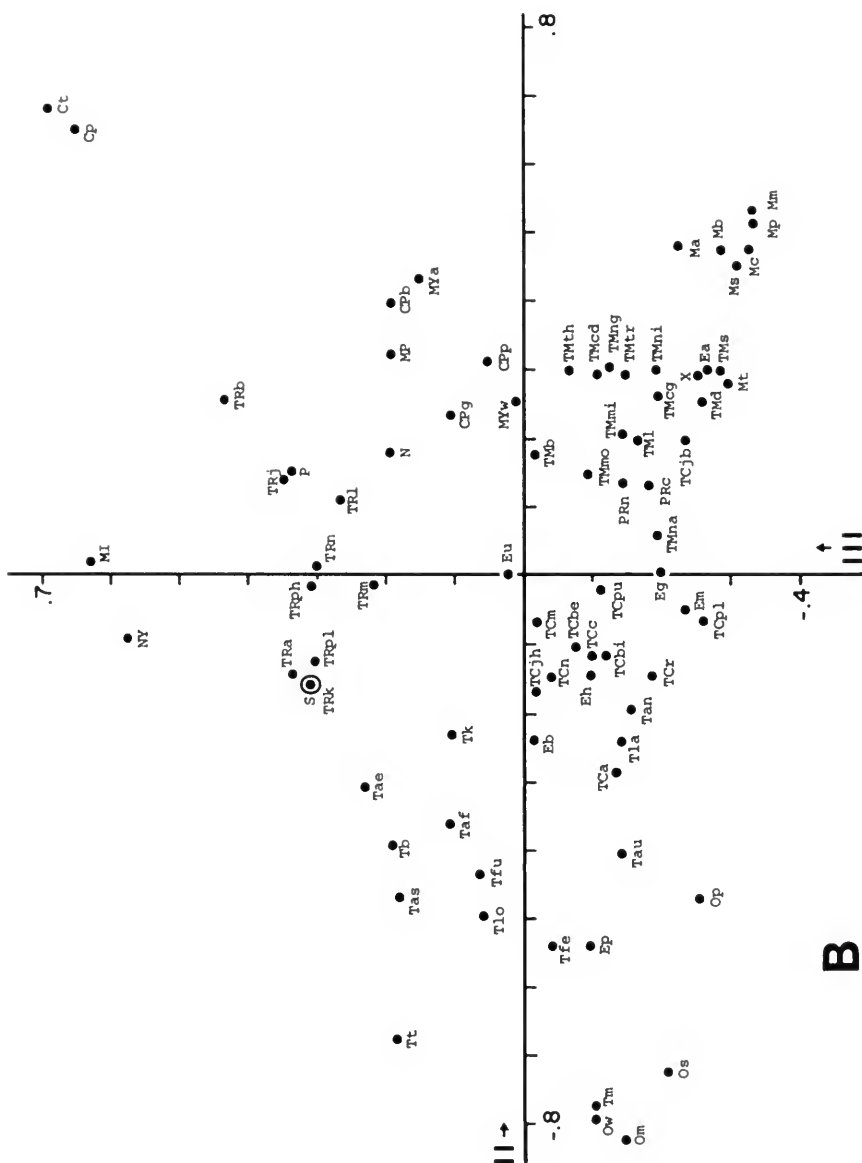


FIGURE 4.



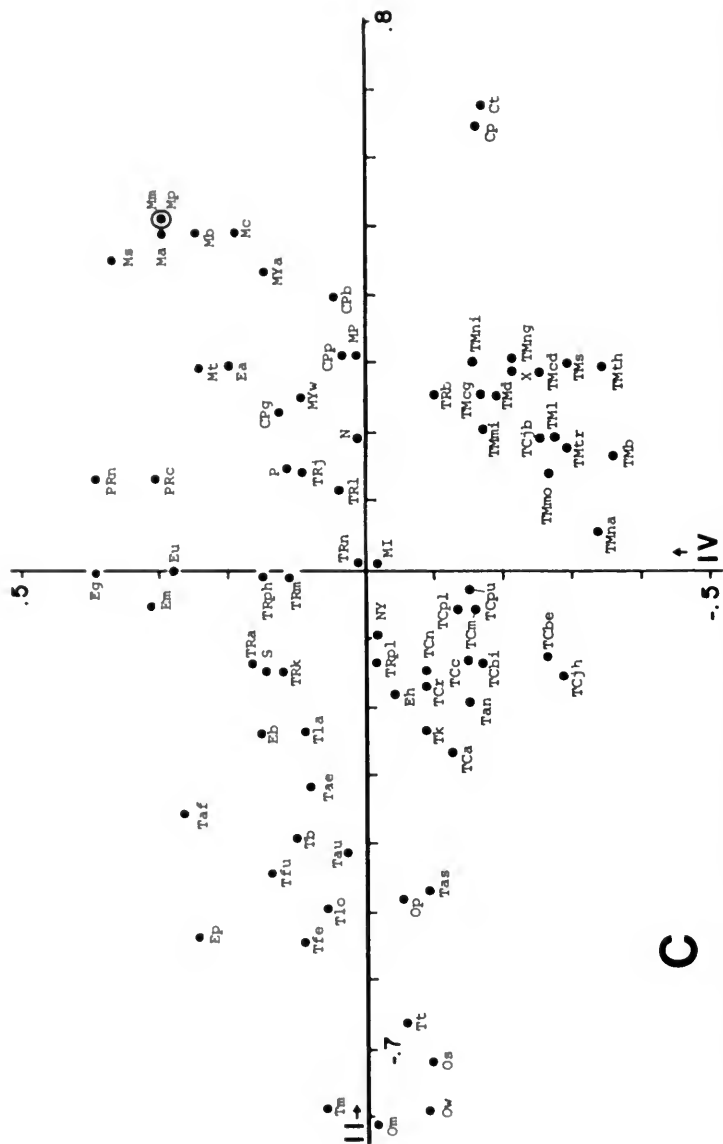


FIG. 4. Three- and two-dimensional graphs of the jaw component (PC II) and components III and IV. Abbreviations are listed in Materials and Methods. A, PC II versus PC III; B, PC II versus PC IV; and C, PC II versus PC IV.

Principal components III and IV are more obscure in their meaning than components I and II. There are fewer highly correlated characters in each, and each accounts for less of the total variation. In general, bats on the negative end of axis III (fig. 4A) have ears facing forward and joined above the nose, well-developed anterior sagittal crest, little development of the coronoid process, deep basisphenoid pits, and faces narrow at the interorbital width. Bats on the positive end generally have widely separated, laterally facing ears, well-developed coronoid processes, shallow basisphenoid pits, and wide faces.

On the fourth component, bats with a well-developed lateral lambdoidal crest and short second phalanx of digit IV are on the positive end, and bats with an undeveloped crest and long phalanx are on the negative end (fig. 4B). If the bats are not extreme in both characters, they are not represented well on this component.

FUNCTIONAL MORPHOLOGY

The jaw structure in molossids is variable: New World extremes are *Molossus ater* on one end, with a short, stout mandible and well-developed sagittal crest; and *Tadarida macrotis* on the other, with a long, delicate mandible and an undeveloped sagittal crest. Likewise, molossids in the Old World have a similar pattern of variation: *Cheiromeles* on the same end with *Molossus ater*; and *Otomops*, with *Tadarida macrotis* (figs. 4, 5). Evidence that I present with each molossid group indicates that the short, thick-jawed bats are eating hard-shelled foods, and the long, delicate-jawed ones are eating soft-shelled items.

Bone thickens at points where more stress occurs (Hildebrand, 1974, pp. 431–456). Maynard Smith & Savage (1959) pointed out that carnivores which take struggling prey have thickened dentaries. Along with this dentary thickening, carnivores also have an increase in the bulk and area of origin of the *m. temporalis*. Some molossid bats, such as *Molossus*, show the same attributes, namely an increased dentary thickness and a well-developed sagittal crest. Molossids of this type also have a greater area of insertion for *m. temporalis* at the coronoid process and possibly an increased area for insertion of the masseter (or leverage) onto the more laterally flaring angular process. Both jaw muscles in *Molossus ater* are developed to a tremendous extent compared with those in *Tadarida macrotis* (fig. 6). The temporal muscle of the first bat nearly encases the braincase from the eye socket to the lambdoidal crest, and the masseter forms a fat, fistlike muscle at the cheek. *Tadarida macrotis*, on the other hand, has no such development of those muscles. The Old World extremes, *Cheiromeles* and *Otomops*, have similar differences in muscle development.

Another characteristic on the second principal component which seems important functionally but is more difficult to explain is the relative height of the mandibular condyle above the lower toothrow. Though this trait is correlated with increasing dentary thickness ($r = .502$), it seems to be greatest in the small bats. Regression analyses in Figure 7 better illustrate these traits as especially characteristic of the small *Mormopterus* and *Mormopterus*-like bats. In carnivores, the condyle is in line with the toothrow, whereas in herbivores, the condyle is well above the toothrow (Maynard Smith & Savage, 1959; Crompton & Heilmäe, 1969). Supposedly, in herbivores, the elevated condyle gives a more uniform bite force along the toothrow (Crompton & Heilmäe, 1969). Storch (1968) and Kallen & Gans (1972) mentioned that the angle of approach of lower

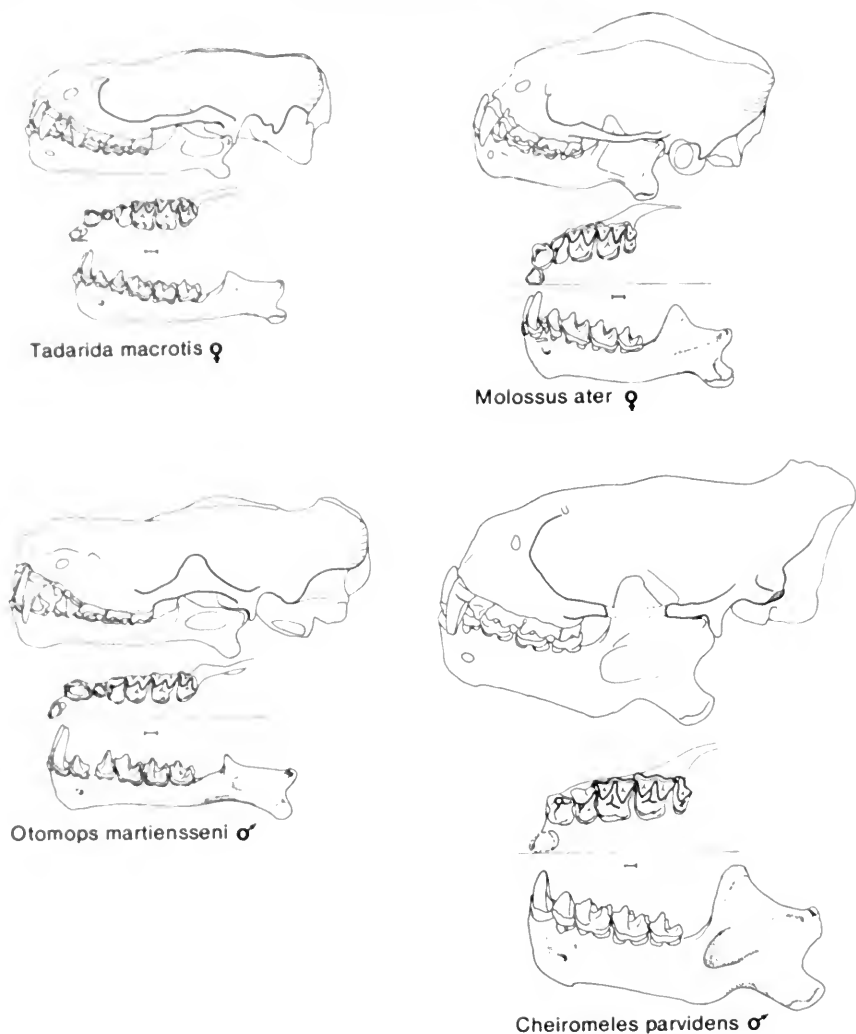
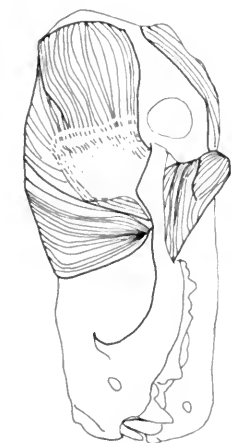
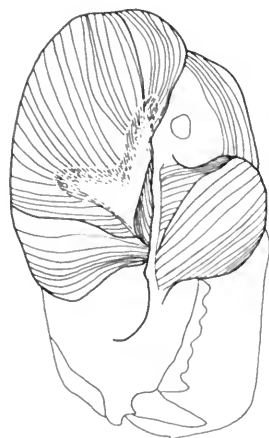


FIG. 5. Four molossids which are opposite extremes on PC II. Shown are the left lateral view of skull, occlusal view of right upper tooththrow, and lateral view of left mandible. *Tadarida macrotis* and *Molossus ater* are New World species; *Otomops martiensseni* and *Cheiromeles parvidens* are Old World species.

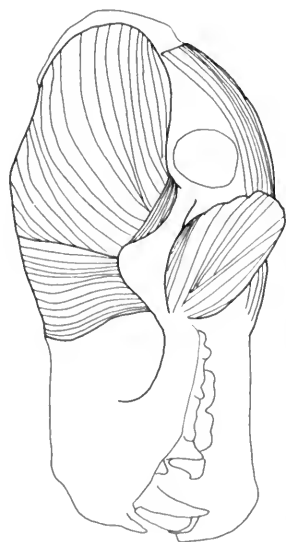
teeth to upper teeth takes a more dorso-anteriad direction rather than a strictly dorsal approach which occurs in those animals where the condyle is in line with the tooththrow. Storch (1968) claimed this angle of attack "produced a better rendering of the food." Whatever the advantage of the elevated condyle, apparently bats with the thickest jaws, as well as the smallest bats, share the condition. Perhaps the hard exoskeleton of a beetle is best processed by the bats with elevated mandibular condyles.



Tadarida macrootis ♀



Molossus ater ♀



Otomops martiensseni ♂



Cheiromeles parvidens ♂

FIG. 6. Jaw muscles of the same four molossids shown in Figure 5.

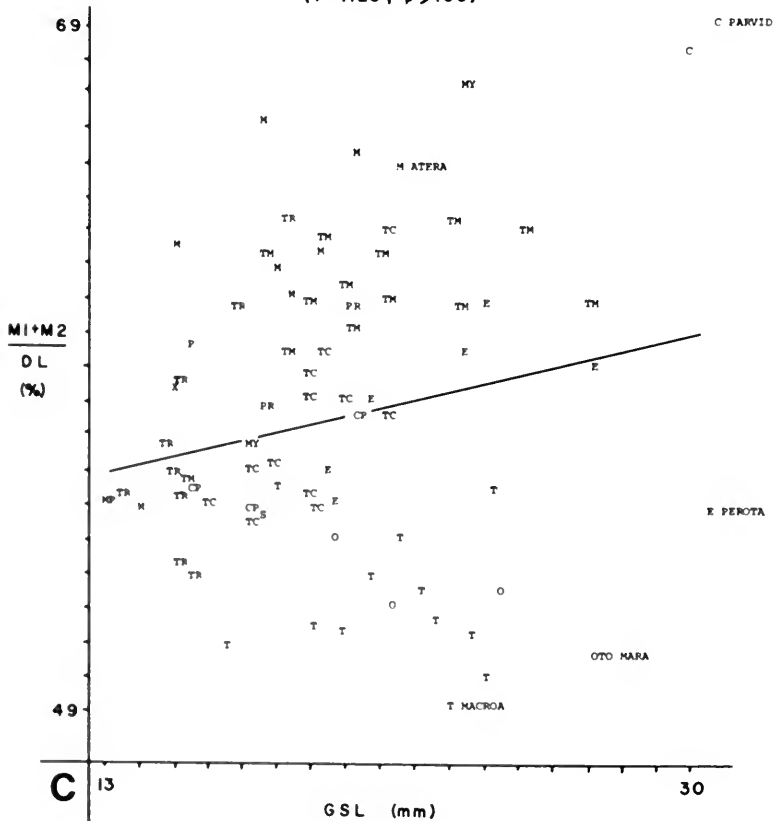
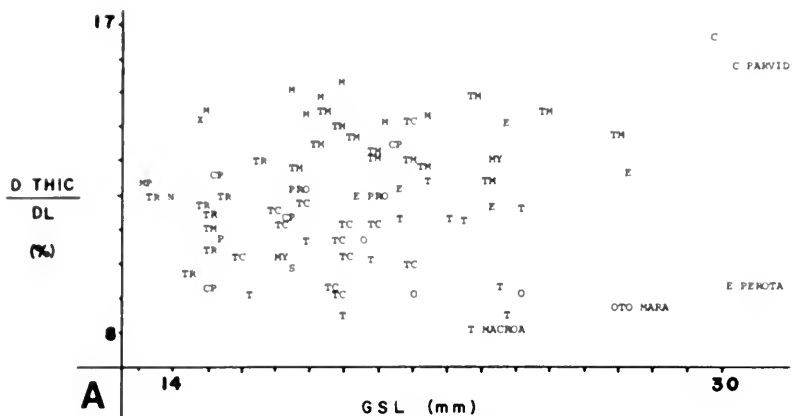


FIGURE 7.

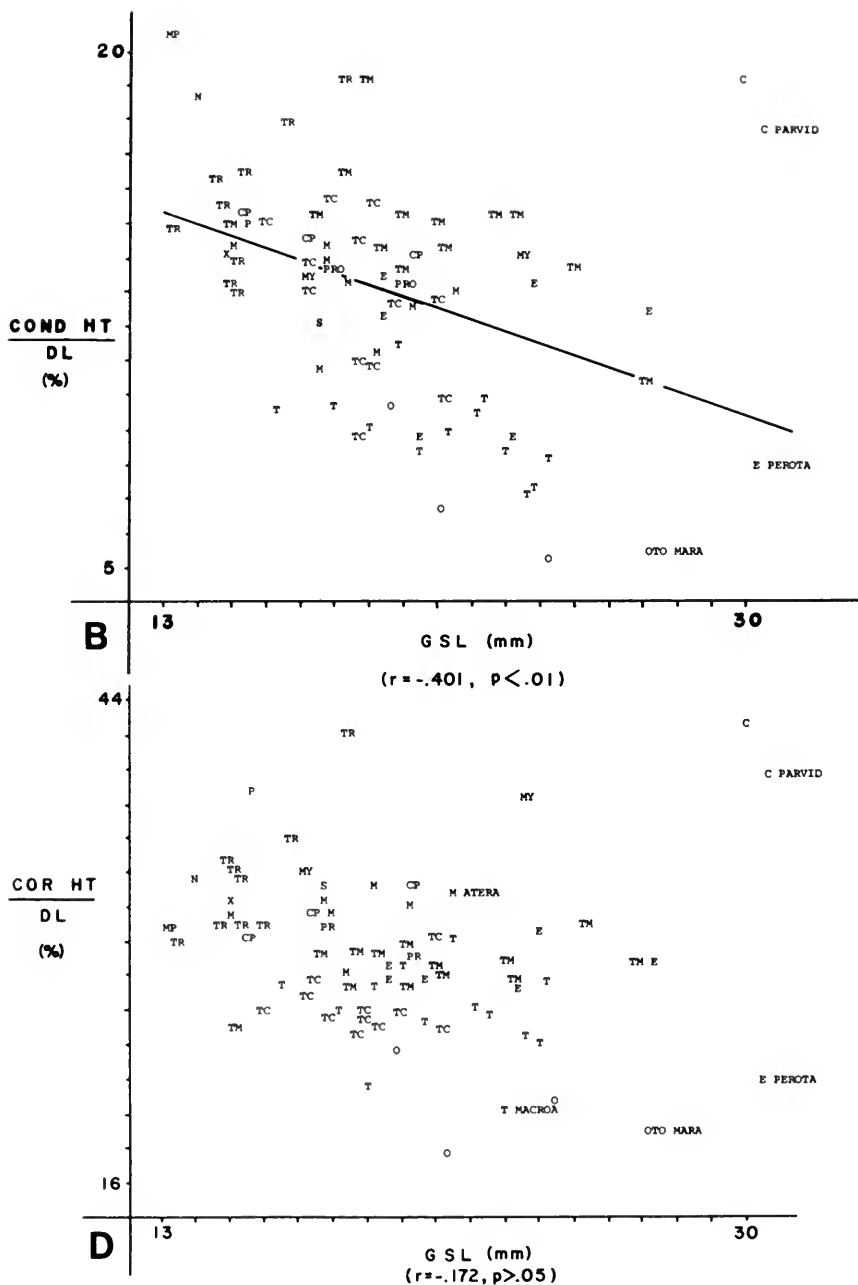


FIG. 7. Regressions of four highly correlated jaw ratios with greatest skull length, a character representing general size. The fact that A, C, and D are not statistically significant is important; that is, relative dentary thickness, moment arm index, and coronoid height do not increase as size increases. A, Relative dentary thickness; B, relative condylar height; C, moment arm index; D, relative coronoid height.

Modifications of upper tooththrows which follow the thick-thin jaw axis have to do with loss of teeth and the general enlargement of the teeth in the tooththrow (fig. 5). *Molossus ater* has lost PM^3 and the posteriormost commissure on M^3 (giving the molar a V-shaped cusp pattern), whereas *Tadarida macrotis* has retained PM^3 and the commissure on M^3 (giving the molar an N-shaped cusp pattern). Although the tooththrows of the two bats are about the same length, the teeth are larger in *M. ater*, and the total length of the cusps is greater in *M. ater* (table 3). As a result, the thick-jawed *M. ater* appears to have a tooththrow, posterior to the canine, of exclusively shearing edges very closely packed together, whereas *T. macrotis*, with its thin dentary, retains PM^3 and a more generalized chewing surface. The fact that species of *Molossus* have lost shearing edges from their M^3 may be the accommodation for shortening the snout and bringing the tooththrow more directly beneath the powerful jaw muscles. The Old World extremes show the same trends.

There are also reductions in the numbers of lower incisors. Corresponding increase in the cingula of the lower canines is related to this loss. *Molossus ater* has only two incisors, *Tadarida macrotis* has four, and *Tadarida brasiliensis* has six, the primitive number (Allen, 1939, p. 162). Incisors in the thin-jawed bats protrude from the dentary more than those in the *Molossus* types, but what function protrusion and increased number of incisors may mean is unknown, although both may have to do with nipping or plucking. The two lower incisors in *Molossus* are virtually nonfunctional.

Gape of the jaws is a character hard to measure on most mammals, although Herring & Herring (1974) have attempted such measurements with trigonometric manipulations. Two jaw characteristics related to gape are the elevation of the condyle above the tooththrow and the height of the coronoid process. The low position of the condyle in carnivores is related to having a wide gape and a powerful bite (Maynard Smith & Savage, 1959; Crompton & Heilmäe, 1969). Supposedly, the animal with the lower coronoid process can open its jaw wider without having that process run into the eye socket (Vaughan, 1972). *Tadarida macrotis* and species of *Otomops*, thin-jawed bats, should have a very wide gape, a feature which would be helpful in taking large insects. I have captured *T. macrotis* alive and found that it does, indeed, have a wide gape.

The third principal component generally separates the bats into two large

TABLE 3. Comparison of upper tooththrow characteristics in five molossids which are opposite extremes on the second principal component.

| Species | Sum cusps M^3-P^4 (mm.) | Sum tooth areas M^3-P^4 (mm. ²) | MTR/ GSL (%) | Cusp row/ MTR (%) | Tooth areas/ MTR ² (%) |
|------------------|------------------------------------|---|--------------------|----------------------------|--|
| <i>T. MACROA</i> | 15.2 | 15.1 | 36.5 | 1.8 | .21 |
| <i>OTO MARA</i> | 15.8 | 18.5 | 37.5 | 1.5 | .18 |
| <i>E. PEROTA</i> | 20.8 | 34.7 | 38.6 | 1.7 | .25 |
| <i>M. ATERA</i> | 17.2 | 20.4 | 36.7 | 2.2 | .30 |
| <i>C. PARVID</i> | 22.5 | 35.9 | 34.6 | 2.1 | .32 |

groups (fig. 4A). Those with large, anteriorly directed ears which join above the nose and deep basisphenoid pits are on one end, whereas those with widely separated, more laterally directed ears and shallow basisphenoid pits are on the other end. A character that covaries with these traits is the degree of wrinkling of the lips as a measure of expandability of the lips. Those species with very expandable lips (either with deep wrinkles or many fine ones) are also the bats with ears joined over the nose and deep basisphenoid pits. The bats opposite these have no wrinkles and less expandable lips.

I believe these third component features point to two basically different ways in which molossids feed. Peterson (1969) and Valdivieso et al. (1979) think the deep basisphenoid pits are related to the echolocating abilities of the bat. Deep basisphenoid pits, along with the large anteriorly directed ears, and expandable lips could mean that a bat has the ability to detect and capture single, large prey. Most of the bats having these attributes, in addition to their more gracile skull and jaws, I suspect of eating soft-bodied creatures like moths. The low coronoid process and low condyle fit neatly into this pattern, because such features would allow a large gape of the jaw, a characteristic probably important in taking large but soft prey.

Bats at the opposite extreme feed in a different way, probably detecting prey differently with their smaller, laterally directed ears and shallow basisphenoid pits. Once detected, I think prey are handled differently, perhaps more swiftly. With fewer or no wrinkles on the lips, these bats may not manipulate prey as well, but because of a higher coronoid and an elevated condyle, they may consume hard or soft-shelled prey faster and more forcefully.

The wrinkling on the lips of many molossids has been the subject of some speculation. Vaughan (1966) suggested that molossids with such lips may fly through the air with their mouths open and lips flaring like a funnel to catch many little insects. Maybe, but I think the wrinkles mean the lips are expandable and aid in the manipulation of prey items. *Tadarida macrotis* has deeply wrinkled lips. When fed several mealworms in succession, this bat does not appear to chew each one and swallow it, but keeps all of them in its lips and cheeks until they are bulging and then processes the whole mass. Not all expandable lips are marked by deep wrinkles; some are skirtlike in appearance and have fine, microscopic wrinkles. *Eumops perotis* is one of this latter variety, along with species of *Otomops* and the large African *Tadarida*. I have seen *Eumops perotis* feeding on crickets. The lips are prehensile and hold the inedible parts, like the femora and head, which are snipped off while the rest of the cricket is consumed. Finally the inedible parts, which have remained in the lips or cheeks, are spit out. That these bats have the ability to hold and manipulate prey with the lips while flying seems a reasonable speculation. It would be interesting to see how a bat on the opposite end of the axis catches and handles prey. Also, the wrinkled lips may be related to how the bat emits sounds, as molossids are known to be oral sound emitters.

The fourth principal component indicates that a wing character, the second phalanx of digit IV, is an important character of variation among molossids. In comparison with other wing characters—such as the indices of Findley et al. (1972), aspect ratio and tip index, or the wing index of Fenton (1972), metacarpal III/metacarpal V—the relative length of the phalanx of the total length of digit IV is far more variable (table 4). Although the three indices mentioned are distinctive for the family, they tell nothing of the variation within the family. The

TABLE 4. Comparison of selected wing characters: relative length of the second phalanx of digit IV, aspect ratio, tip index, and digit III/digit V ratio (aspect ratio and tip index are taken after Findley et al., 1972; digit III/digit V ratio, after Fenton, 1972). Species are arranged by genus and are ordered according to increasing relative length of the second phalanx of digit IV.

| <u>Tadarida</u> | | | | | <u>Chaerophon</u> | | | | |
|-----------------|----------------------|--------|----------|-------|-------------------|----------------------|--------|----------|-------|
| | 4M 2PHAL DIGIT IV | ASPECT | TIP INDX | D3/D5 | | 4M 2PHAL DIGIT IV | ASPECT | TIP INDX | D3/D5 |
| T MACROA | 3.10 | 2.94 | 64.93 | 1.90 | TC ALOYA | 14.40 | 2.94 | 66.54 | 1.96 |
| T FEMORA | 3.70 | 2.96 | 66.79 | 1.98 | TC BIVIA | 14.40 | 2.93 | 66.91 | 1.96 |
| T AURISA | 3.75 | 2.91 | 66.69 | 1.94 | TC RUSSA | 14.84 | 2.92 | 67.58 | 1.98 |
| T LATICA | 4.25 | 2.86 | 65.35 | 1.87 | TC PLICA | 15.58 | 2.82 | 66.20 | 1.87 |
| T AFRICA | 9.16 | 2.78 | 65.80 | 1.83 | TC BENMI | 15.59 | 2.85 | 66.90 | 1.91 |
| T FULMIN | 9.28 | 2.92 | 65.57 | 1.91 | TC JOHOR | 15.71 | 3.03 | 66.74 | 2.02 |
| T LOBATA | 10.66 | 2.72 | 66.44 | 1.81 | TC MAJOR | 16.52 | 2.88 | 66.50 | 1.92 |
| T AEGYPA | 11.23 | 2.83 | 65.70 | 1.86 | TC JOBEN | 16.58 | 2.97 | 66.71 | 1.98 |
| T TENIOA | 12.00 | 2.86 | 66.05 | 1.89 | TC NIGEA | 17.03 | 2.84 | 67.23 | 1.91 |
| T BRASIA | 12.67 | 2.79 | 65.65 | 1.83 | TC PUMIA | 17.68 | 2.72 | 67.41 | 1.84 |
| T ANSORA | 14.53 | 2.90 | 66.88 | 1.94 | TC CHAPI | 17.72 | 2.86 | 66.10 | 1.89 |
| T KUBORI | 17.14 | 2.97 | 66.28 | 1.97 | | | | | |
| T AUSTRA | 17.35 | 2.85 | 66.21 | 1.88 | | | | | |

| <u>Mops</u> | | | | | <u>Mormopterus-Sauromys-Platymops</u> | | | | |
|-------------|----------------------|--------|----------|-------|---------------------------------------|----------------------|--------|----------|-------|
| | 4M 2PHAL DIGIT IV | ASPECT | TIP INDX | D3/D5 | | 4M 2PHAL DIGIT IV | ASPECT | TIP INDX | D3/D5 |
| TM CONGA | 12.24 | 2.97 | 67.80 | 2.01 | TR PHRUD | 9.40 | 2.63 | 64.96 | 1.71 |
| TM NIANG | 13.80 | 2.98 | 67.23 | 2.01 | TR KALIN | 13.26 | 2.71 | 64.46 | 1.75 |
| TM TREVO | 13.92 | 2.98 | 67.65 | 2.02 | TR MINUP | 14.19 | 2.53 | 65.64 | 1.66 |
| TM LEONA | 15.00 | 2.71 | 66.00 | 1.79 | TR JUGUA | 15.74 | 2.84 | 64.51 | 1.83 |
| TM SAUSA | 15.09 | 3.02 | 66.42 | 2.00 | TR BECCR | 15.80 | 2.77 | 66.28 | 1.83 |
| TM MOPSA | 15.77 | 2.87 | 65.80 | 1.89 | TR ACETA | 16.12 | 2.48 | 65.19 | 1.61 |
| XIPHONYC | 16.70 | 2.76 | 65.11 | 1.80 | TR PLANA | 18.21 | 2.65 | 67.00 | 1.78 |
| TM NANUA | 16.81 | 2.85 | 66.36 | 1.83 | TR LORIA | 18.59 | 2.61 | 68.35 | 1.79 |
| TM MIDAA | 16.88 | 2.85 | 66.85 | 1.91 | TR NORFA | 18.75 | 2.67 | 66.84 | 1.78 |
| TM NIVEI | 17.26 | 2.87 | 67.00 | 1.92 | | | | | |
| TM DEMOA | 17.40 | 2.72 | 66.95 | 1.82 | SAUROMYS | 11.39 | 2.56 | 66.11 | 1.69 |
| TM BRACH | 17.44 | 2.80 | 68.31 | 1.92 | PLATYMOP | 17.40 | 2.42 | 66.67 | 1.61 |
| TM THERA | 17.93 | 2.84 | 67.28 | 1.91 | | | | | |
| TM CONDA | 19.77 | 2.82 | 68.58 | 1.93 | | | | | |

length of the second phalanx varies between 3 and 20 per cent of the total length of the fourth digit. All molossids are thought to be fast fliers (Vaughan, 1959, 1966; Hartman, 1963; Struhsaker, 1961; Findley et al., 1972; Fenton, 1972), and are correspondingly set apart from other bat families. Variability in the last phalanx of digit IV may mean that, although molossids are fast, there is further gradation in the degree of swiftness and maneuverability within the already fast-flying family. I believe short length in this character is related to a narrow wing tip, resulting in faster, less maneuverable flight, whereas the long phalanx means a broader tip, more camber, more maneuverability, and possibly less speed. Bats with the narrow tips should fly in more open areas, and those with broad tips should be in areas with more obstacles, trees of a forest or possibly walls of a cave.

TABLE 4. Continued.

| <u>Conglomerate-Cheiromeles</u> | | | | | <u>Eumops</u> | | | | |
|---------------------------------|------------------------------------|--------|----------|-------|--|------------------------------------|--------|----------|-------|
| | <u>4M 2PHAL</u> <u>DIGIT IV</u> | ASPECT | TIP INDX | D3/D5 | | <u>4M 2PHAL</u> <u>DIGIT IV</u> | ASPECT | TIP INDX | D3/D5 |
| CP GREEA | 6.87 | 2.86 | 66.40 | 1.90 | E HANSAA | 5.54 | 3.01 | 65.11 | 1.96 |
| CP BRACA | 7.49 | 2.87 | 67.96 | 1.95 | E PEROTA | 5.73 | 2.88 | 68.41 | 1.92 |
| CP PLANA | 8.50 | 2.83 | 67.15 | 1.90 | E GLAUCA | 6.40 | 2.94 | 66.43 | 1.95 |
| NEOPLATA | 12.34 | 2.48 | 65.75 | 1.63 | E BONARA | 6.59 | 2.70 | 66.90 | 1.81 |
| MYOP WHA | 17.10 | 2.64 | 66.91 | 1.77 | E AURIPA | 6.90 | 3.04 | 67.43 | 2.05 |
| MYOP ALB | 17.20 | 2.70 | 67.08 | 1.80 | E UNDERA | 7.14 | 2.87 | 67.79 | 1.95 |
| MP TEMMA | 19.92 | 2.50 | 67.02 | 1.68 | E MAURUS | 7.80 | 2.93 | 66.54 | 1.95 |
| | | | | | | | | | |
| C PARVID | 16.60 | 3.13 | 70.23 | 2.20 | | | | | |
| C TORQUT | 17.12 | 3.14 | 69.95 | 2.19 | | | | | |
| | | | | | | | | | |
| <u>Molossus</u> | | | | | <u>Otomops-Promops-Vespertilionids</u> | | | | |
| | <u>4M 2PHAL</u> <u>DIGIT IV</u> | ASPECT | TIP INDX | D3/D5 | | <u>4M 2PHAL</u> <u>DIGIT IV</u> | ASPECT | TIP INDX | D3/D5 |
| M PRETIA | 4.50 | 3.00 | 65.82 | 1.97 | OTO SECA | 11.50 | 2.99 | 64.54 | 1.93 |
| M COIBEIA | 4.60 | 2.90 | 67.34 | 1.95 | OTO PAPU | 12.60 | 2.90 | 64.96 | 1.88 |
| M BONDAA | 4.80 | 2.86 | 66.86 | 1.91 | OTO MARA | 12.95 | 2.85 | 65.19 | 1.86 |
| M ATERA | 4.84 | 2.85 | 66.36 | 1.89 | OTO WROA | 13.20 | 2.89 | 65.32 | 1.89 |
| M MOLOSS | 5.40 | 2.79 | 66.61 | 1.86 | | | | | |
| M SINALA | 5.60 | 2.81 | 65.90 | 1.85 | PRO NASU | 4.30 | 2.64 | 67.03 | 1.78 |
| M TRINIT | 6.10 | 2.82 | 66.82 | 1.88 | PRO CENA | 4.40 | 2.82 | 67.21 | 1.90 |
| | | | | | | | | | |
| | | | | | MIMETILL | 4.46 | 2.41 | 62.23 | 1.50 |
| | | | | | NYCTALUS | 9.30 | 2.64 | 65.24 | 1.72 |

The functional significance of size in these bats has several obvious ramifications. Larger bats probably take larger prey and require larger places to roost, whereas smaller bats take smaller items and can live in smaller roosting places. A size difference between males and females of the same species is common, with the males usually being larger. Besides size, males have larger canines and larger cranial crests, but why these sexually dimorphic differences occur has not yet been determined.

Certain patterns, however, appear among small bats alone or large bats alone. For example, some of the smaller bats seem to feed on both hard and soft items whether they have thick or thin jaws. Thompson (1971) mentioned that smaller animals are stronger, proportionally, than larger ones because muscle power varies by the square of linear dimensions, whereas volume varies by the cube. Also, patterns in tooth loss and jaw structure and wing configuration in the smaller bats are discussed in the sections concerned with the morphological features of the groups.

Large congeners are thought to be allometric with respect to small congeners. That is, they are out of proportion with the smaller animal and are not merely photographic, or isometric, enlargements of that shape. Several groups of molossids appear to have a more predictable allometric relationship between small and large congeners. In *Mops* and *Molossus*, size seems to be the only thing which separates the species, and shape seems to change very little. These

genera are also two which have lost teeth and cusps and are suspected of concentrating on hard-shelled food items.

MORPHOMETRIC DESCRIPTIONS OF GROUPS

Placement of the 80 OTU's onto the principal components is illustrated in Figure 4 where components II, III, and IV, only, are shown. Component I, which is size-related, has been omitted. Starting with the more compact clusters of bats, I discuss each OTU with respect to: 1) position in the PCA; 2) relationships in the three clustering analyses (distance, size-in and size-out, and correlation); 3) size and functional interpretations; 4) possible ecological capabilities; and 5) natural history support or nonsupport for the predictions made by the analysis.

Several of the classical genera or subgenera form distinct clusters in this analysis. Results of my study often substantiate and quantify classical observation. Until I restrict it further, I use the name *Tadarida* to mean what is now *Tadarida* (*Tadarida*), including both Old and New World species. Only if *Tadarida* (*sensu lato*) is used does the name include all subgenera of *Tadarida*. Likewise, I treat *Chaerephon*, *Mops*, and *Mormopterus* as genera, not subgenera, of *Tadarida*.

In the three space components II, III, and IV, several groups appear as compact entities. These groups are *Cheiromeles*, *Molossus*, *Mops*, *Chaerephon*, and finally, a group of three species of *Otomops* plus *Tadarida macrotis*. The remaining bats form no distinctly isolated clusters. The least compact group of species, supposedly belonging to a single taxon, are species of the genus *Eumops*. Average least distances among species within classical taxa or groups formed by this study quantify the dispersion in each (table 5). I arbitrarily designate the mean least distance of the two distance matrices (size-in and size-out) as the dividing points below which taxa are considered compact and above which taxa are considered dispersed. Although five of the groups which form compact clusters on the PCA are also considered compact in table 5 (*Cheiromeles*, *Molossus*, *Mops*, *Chaerephon*, and *Otomops*), there are several other compact groups derived from the distance matrix which do not appear as distinct entities on the PCA (*Cynomops*, *Promops*, and *Mormopterus*). The PCA gives an overview of the phenetic resemblance of all the bats; distance and correlation determine the closest morphological neighbors of each species. All of the groups (genera and subgenera) I use in the following morphological analysis have nearest neighbors within the group. The phenogram of the size-out distance matrix presented in the final section on evolution summarizes the phenetic relatedness of all the species in the groups. The groups I use here are mostly classical taxa and are convenient for explanation. In the final section, I modify these groups into what I think are the natural genera of the family.

I use the size-out distance matrix extensively to quantify what can be seen in the three- and two-dimensional plots representing the PCA (fig. 4). Nearest neighbors within a taxon (genus or subgenus) can be taken from the matrix, but nearest neighbors among taxa have a more complicated derivation (fig. 8). As an example, taxon J has three species, a, b, and c; and taxon K has three species, d, e, and f. The distance from a to d, e, and f can be obtained and averaged as can that from b to d, e, and f; and c to d, e, and f. In turn, a's average distance to K, b's average distance to K, and c's average distance to K can all three be summed together and averaged. The result is the average distance from J to K or

TABLE 5. Average least distances of members within a taxon for both size-in and size-out distance (averages below the mean of each matrix are considered compact; those above, dispersed).

| SIZE-OUT | | SIZE-IN | |
|---------------------------|------|---------------------|-------|
| <u>Cheiromeles</u> | .278 | <u>Cheiromeles</u> | .301 |
| <u>Cynomops</u> | .304 | <u>Molossus</u> | .437 |
| <u>Promops</u> | .313 | <u>Mormopterus</u> | .437 |
| <u>Molossus</u> | .328 | <u>Chaerephon</u> | .441 |
| <u>Mops</u> | .385 | <u>Mops</u> | .458 |
| <u>Otomops</u> | .390 | <u>Mormopterus</u> | .475 |
| <u>Chaerephon</u> | .364 | <u>Sauromys</u> | |
| <u>Mormopterus</u> | .384 | <u>Platymops</u> | |
| <u>Mormopterus</u> | .416 | <u>Molossops</u> | .492 |
| <u>Sauromys</u> | | <u>Neoplatymops</u> | |
| <u>Platymops</u> | | | |
| Mean least | .420 | Mean least | .508 |
| distance of matrix | | distance of matrix | |
| <u>Molossops</u> | .423 | <u>Otomops</u> | .535 |
| <u>Neoplatymops</u> | | <u>Promops</u> | .559 |
| <u>Cynomops</u> | | <u>Tadarida</u> | .562 |
| New World <u>Tadarida</u> | .443 | <u>Cynomops</u> | .570 |
| (excl. T BRASIA) | | <u>Eumops</u> | .607 |
| Old and New World | .458 | <u>Myopterus</u> | 1.489 |
| <u>Tadarida</u> | | | |
| Old World <u>Tadarida</u> | .464 | | |
| (incl. T BRASIA) | | | |
| <u>Molossops</u> | .491 | | |
| <u>Neoplatymops</u> | | | |
| <u>Myopterus</u> | .528 | | |
| <u>Eumops</u> | .560 | | |

the average distance between supraspecific taxa. If the average distance, J to K, is the smallest average distance value of J to any other taxon, then the J-K value is the least average, and K is J's nearest neighboring taxon. From these values, least and greatest averages, or nearest and farthest neighbors, for each genus or subgenus are taken.

Molossus

Molossus is a genus of New World bats that is found mostly south of the Tropic of Cancer and here includes the species *M. ater*, *M. bondae*, *M. coibensis*, *M. molossus*, *M. sinaloae*, *M. pretiosus*, and *M. trinitatus*. Species of the genus are distinctly clustered and isolated from other bats in the PCA (fig. 4) and tend to be extreme on the shape-related components. Members of the genus *Molossus* have a heavy build, mastiff appearance, thick jaws, and narrow wing tips. Their

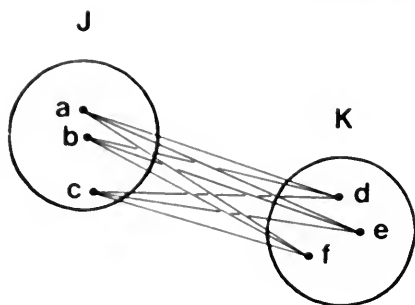


FIG. 8. Diagrammatic scheme of calculating the average distance among taxa. Taxa are J and K; species are a, b, c, d, e, and f; and \bar{x} is the average distance from J to K. If \bar{x} is the smallest distance value of J to any other taxa, then \bar{x} is the least average distance and K is the nearest taxa to J.

ears are neither completely separated nor fully joined over the nose. Average relative dentary thickness is 14 per cent of dentary length, whereas the average percentage that the second phalanx comprises of digit IV is 5 per cent (table 6). Other jaw-related characters include: well-developed sagittal and lambdoidal crests and coronoid process, condyle well above the toothrow (the mean is 13 per cent of dentary length), diminution of the last upper molar (V-shape), and absence of the third upper premolar (fig. 9, appendix A).

Molossus trinitatus, a slightly outlying species on axis II, is not as robust as other *Molossus* in some jaw and skull features, such as relative coronoid height and development of sagittal and lambdoidal crests. *Eumops auripendulus*, a very robust species, is close to the *Molossus* cluster on the PCA (fig. 4). I treat it as a *Molossus*-like *Eumops* rather than as a *Eumops*-like *Molossus* and discuss it in the *Eumops* section.

There is no species of *Molossus* that is not a nearest neighbor to or most highly correlated with a congener in the three clustering methods (table 7). The genus is a very compact group in the family and has a relatively small average least distance (size-out) among its species (0.328), well below the point demarcating compact and dispersed groups. *Molossus* is a compact group even when size is included (0.437), being second only to *Cheiromeles* (table 5).

As for nearest neighbors among taxa (table 8), the nearest genus to *Molossus* is *Promops* (0.687), whereas the farthest genus is *Otomops* (1.331). These near and far genera correspond well with the placement of the three genera in the PCA.

Greatest skull length among the seven species of *Molossus* dealt with here ranges from 15.0 mm in *M. coibensis* to 21.5 mm in *M. ater* (table 1). There are no extremely small or large *Molossus*. There seem to be few changes in shape among species as the species get larger, and I suspect the allometric relationship between small and large congeners is more predictable than that in other genera.

TABLE 6. Six important characters (in percentages) as indicated by the PCA and ordered from least to greatest (*Mormopterus* and Conglomerate contain the same taxa as listed in Table 1).

[illegible]

TABLE 6. Continued.

| Taxafida | Characterization | Moya | Mozambique | Conglomerate | Eumya | Molossus | Oromys | Promys |
|---------------|------------------|---------------|----------------|---------------|---------------|---------------|---------------|----------------|
| | | | | | | | | |
| T MACRO 49.1 | TC MAJOR 54.5 | TH MANIA 55.6 | TR PHUD 52.7 | CP GRECA 54.8 | E PEROTA 54.8 | M TRINIT 61.2 | OTO MABA 50.5 | PMO MASU 57.8 |
| T TETRA 50.0 | TC CHAPT 55.0 | XIPHONT 58.5 | TR KALIN 53.3 | MDPLATA 55.1 | E BORDAA 55.1 | M BORDAA 61.9 | OTO BECA 52.2 | PMO CENIA 60.3 |
| T BASTIA 50.9 | TC JORON 55.0 | TH BACH 59.4 | SAURONT 54.8 | MP TEMPA 55.1 | E HANISA 56.0 | M BIMALA 62.4 | OTO MICA 52.6 | |
| T AUSTRA 51.3 | TC HICCA 55.3 | TH CHIDA 60.1 | TR PLANA 55.1 | CP PLANA 55.1 | E MAURIS 58.1 | M COIREA 62.5 | OTO PAPU 54.0 | |
| T AUSTRA 51.4 | TC PUNIA 56.0 | TH TREVO 60.7 | TR MINIA 55.3 | MYOP MIA 56.8 | E UNDEKA 59.0 | M ATERA 64.7 | | |
| T PUNIA 51.5 | TC BEHPI 56.2 | TH THEKA 60.8 | TR LORIA 55.8 | CP BIRCA 57.6 | E GLAUCA 59.5 | M PRETIA 65.3 | | |
| T LORATA 51.9 | TC ALOTA 57.7 | TH MIDAA 60.9 | TR ACETA 56.7 | MYOP ALB 67.3 | E AURIPA 60.7 | M MOLLOS 66.1 | | |
| T PUNIA 52.5 | TC BIVTA 58.1 | TH MOISA 61.0 | TH MOISA 58.5 | C TOROUT 68.2 | | | | |
| T AUSTRA 52.8 | TC RUBIA 58.9 | TH DEKCA 61.4 | PLATMOP 59.6 | C PARVID 69.0 | | | | |
| T KUBORI 54.1 | TC PELCA 59.4 | TH LORNA 62.2 | TR JUCCA 60.7 | | | | | |
| T AFRICA 55.4 | TC JORON 62.8 | TH NYVEI 62.2 | TR BECCIN 63.4 | | | | | |
| T LATICA 55.6 | | TH BARSA 62.7 | | | | | | |
| T ANSOLA 58.1 | | TH CONCA 62.9 | | | | | | |
| | | TH NIANG 63.2 | | | | | | |

| Taxafida | Characterization | Moya | Mozambique | Conglomerate | Eumya | Molossus | Oromys | Promys |
|---------------|------------------|---------------|----------------|---------------|---------------|---------------|---------------|----------------|
| | | | | | | | | |
| T MACRO 20.1 | TC ALOTA 24.6 | TH MANIA 25.0 | TR MINIA 29.8 | CP PLANA 30.4 | E PEROTA 22.8 | M TRINIT 27.9 | OTO BECA 17.9 | PMO CENIA 28.7 |
| T PUNIA 21.2 | TC PELCA 26.0 | TH DEKCA 27.1 | TR ACETA 30.8 | MP TEMPA 30.6 | E GLAUCA 27.2 | M COIREA 31.3 | OTO MABA 18.8 | PMO MASU 31.0 |
| T TETRA 24.1 | TC BEHPI 25.6 | TH BACH 27.3 | TR KALIN 30.8 | CP GRECA 31.5 | E BORDAA 27.5 | M BORDAA 31.7 | OTO MICA 20.5 | |
| T AUSTRA 24.4 | TC BIVTA 25.7 | TH TREVO 27.6 | TR PHUD 30.9 | CP BIRCA 31.1 | E MAURIS 27.7 | M PRETIA 31.9 | OTO PAPU 23.4 | |
| T ANHONG 24.8 | TC HICCA 25.8 | TH MOISA 28.4 | SAURONT 31.1 | MDPLATA 31.3 | E HANISA 28.4 | M MOLLOS 32.2 | | |
| T AUSTRA 25.0 | TC RUBIA 25.8 | TH NYVEI 28.4 | TR PLANA 31.6 | MYOP MIA 31.9 | E UNDEKA 28.6 | M ATERA 32.7 | | |
| T LATICA 25.8 | TC CHAPT 26.0 | TH MIDAA 28.6 | TR MOISA 34.0 | MYOP ALB 38.6 | | | | |
| T LORATA 25.9 | TC MAJOR 26.8 | TH NIANG 28.8 | TR LORIA 34.6 | C PARVID 39.8 | | | | |
| T PUNIA 26.2 | TC JORON 27.1 | TH BARSA 29.1 | TR JUCCA 35.9 | C TOROUT 42.7 | | | | |
| T BASTIA 27.3 | TC PUNIA 27.6 | TH THEKA 29.2 | PLATMOP 38.6 | | | | | |
| T AFRICA 27.4 | TC JORON 30.1 | TH LORNA 29.4 | TR BECCIN 42.0 | | | | | |
| T AUSTRA 28.6 | | TH CONCA 29.7 | | | | | | |
| T KUBORI 30.2 | | XIPHONT 32.1 | | | | | | |

Relative earcanoid height (cor H/DL)

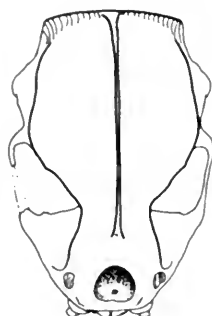
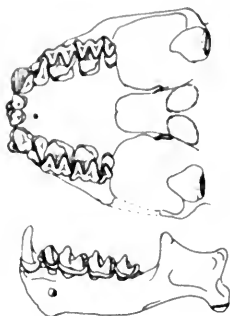
TABLE 6. Continued.

| Relative length of second phalanx of digit IV (4M 2PHAL/DIGIT 4) | | | | | | |
|--|---------------|----------------|---------------|---------------|--------------|--------------|
| Tarsal id | Characterid | NOSE | Molompterus | Conglomerate | Eumops | Promops |
| T MACROA 3.1 | TC ALOVA 14.4 | TM CONGA 12.2 | TR PHRID 9.4 | CP GREZA 6.9 | E HANSAA 5.5 | M PRETIA 4.5 |
| T FEMORA 3.7 | TC BIVIA 14.4 | TM NIANG 13.8 | SAURONIS 11.4 | CP PLANA 7.5 | E PEROTA 5.7 | M COIREA 4.6 |
| T AURISA 3.8 | TC RUSSA 14.8 | TM TREPO 13.9 | TR KALIN 13.3 | CP BRACA 8.5 | E GLAUCA 6.4 | M BORDIA 4.8 |
| T LATICA 4.2 | TC PLICA 15.6 | TM LEONA 15.0 | TR MINUA 14.2 | NEOPLATA 12.3 | E BONARA 6.6 | M ATERA 4.8 |
| T AFRICA 9.2 | TC BECHI 15.6 | TM SANSIA 15.9 | TR JUJUL 15.7 | C PARTID 16.6 | E AURIPA 6.9 | M MOLOS 5.4 |
| T FILAMIN 9.3 | TC JOHOR 15.7 | TM MOFSA 15.8 | TR BECCR 15.8 | C TOROUT 17.1 | E UNDERA 7.1 | M SINALA 5.6 |
| T LOBATA 10.7 | TC MAJOR 16.5 | XIPHONIC 16.7 | TR ACCTA 16.1 | MOF WHA 17.1 | E MAURIS 7.8 | M TRINIT 6.1 |
| T ACCTA 11.2 | TC JOHEN 16.6 | TM NANUA 16.8 | PLATYTOP 17.4 | MOF ALB 17.2 | | |
| T TENIOA 12.0 | TC NIGEA 17.0 | TM MIDAA 16.9 | TR PLANA 18.2 | MP TERMA 19.9 | | |
| T BRASIA 12.7 | TC PUMIA 17.7 | TM NIVEI 17.4 | TR LORIA 18.6 | | | |
| T ANSOBA 14.5 | TC CHAPI 17.7 | TM DENKA 17.4 | TR MOFSA 18.8 | | | |
| T KUBORI 17.1 | | TM BRACH 17.4 | | | | |
| T AUSTRA 17.4 | | TM THERA 17.9 | | | | |
| | | TM CONDA 19.8 | | | | |

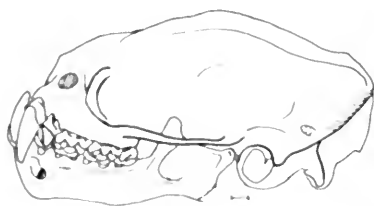
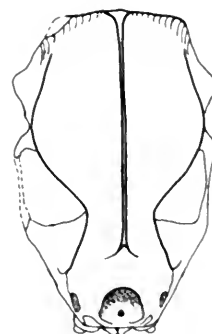
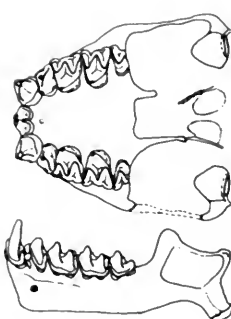
| Relative length of 3 rd (M3 LENG/DL) | | | | | | |
|---|--------------|---------------|---------------|--------------|--------------|--------------|
| Tarsal id | Characterid | NOSE | Molompterus | Conglomerate | Eumops | Promops |
| T AFRICA 6.3 | TC MAJOR 7.3 | TM SANSIA 5.2 | SAURONIS 7.3 | MOF WHA 5.1 | E MAURIS 4.7 | M MOLOS 5.0 |
| T LOBATA 7.4 | TC BIVIA 7.4 | TM DENKA 5.7 | TR BECCR 8.4 | C TOROUT 5.9 | E GLAUCA 5.8 | M SINALA 6.0 |
| T ANSOBA 7.8 | TC NIGEA 7.6 | TM MIDAA 5.7 | TR JUJUL 8.5 | C PARTID 6.2 | E AURIPA 6.3 | M TRINIT 6.2 |
| T AUSTRA 8.1 | TC ALOVA 7.7 | TM MOFSA 5.7 | TR MINUA 8.5 | MOF ALB 6.4 | E PEROTA 7.0 | M BORDIA 6.3 |
| T FILAMIN 8.1 | TC JOHEN 7.7 | XIPHONIC 5.7 | TR ACCTA 8.7 | CP GREZA 6.4 | E UNDERA 7.1 | M COIREA 6.3 |
| T TENIOA 8.2 | TC PLICA 7.8 | TM NIANG 6.1 | PLATYTOP 8.8 | CP BRACA 6.6 | E BONARA 8.7 | M PRETIA 6.3 |
| T AURISA 8.3 | TC RUSSA 8.1 | TM TREPO 6.1 | TR PHRID 9.1 | CP PLANA 7.1 | E HANSAA 9.0 | N ATERA 6.4 |
| T ACCTA 8.6 | TC BECHI 8.3 | TM THERA 6.2 | TR PLANA 9.3 | MP TERMA 8.1 | | |
| T BRASIA 8.8 | TC PUMIA 8.6 | TM CONGA 6.3 | TR MOFSA 9.4 | NEOPLATA 8.8 | | |
| T KUBORI 8.8 | TC CHAPI 9.0 | TM CONDA 6.5 | TR LORIA 9.6 | | | |
| T MACROA 8.8 | TC JOHOR 9.3 | TM NANUA 6.5 | TR KALIN 10.3 | | | |
| T LATICA 8.9 | | TM LEONA 6.7 | | | | |
| T FEMORA 9.1 | | TM NIVEI 6.8 | | | | |
| | | TM BRACH 7.0 | | | | |



Molossus colibensis ♂



Molossus molossus ♂



Molossus bondae ♂

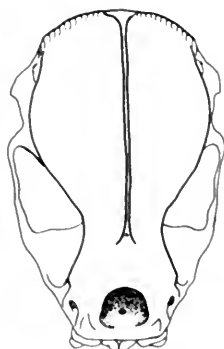
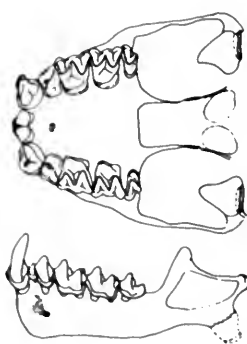
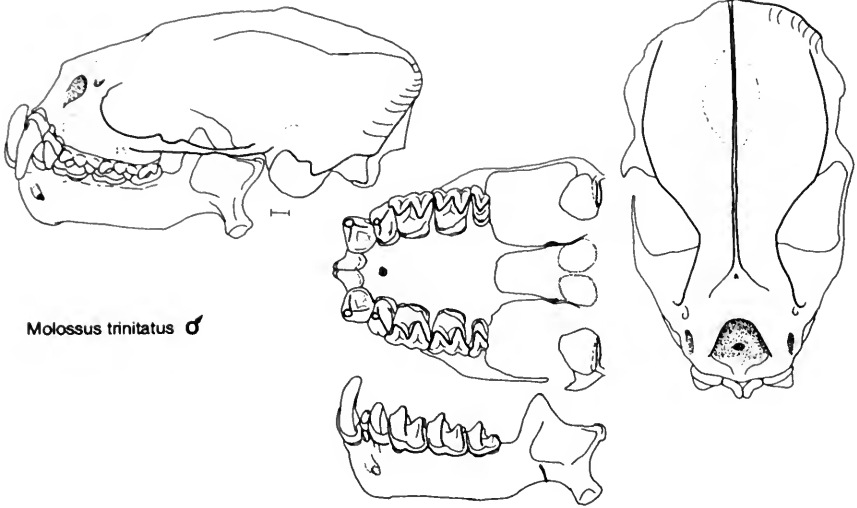
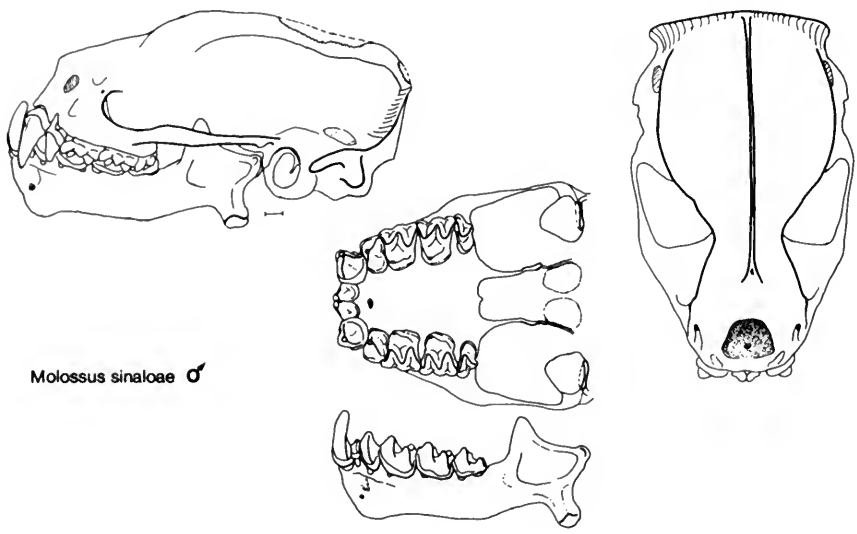


FIGURE 9.

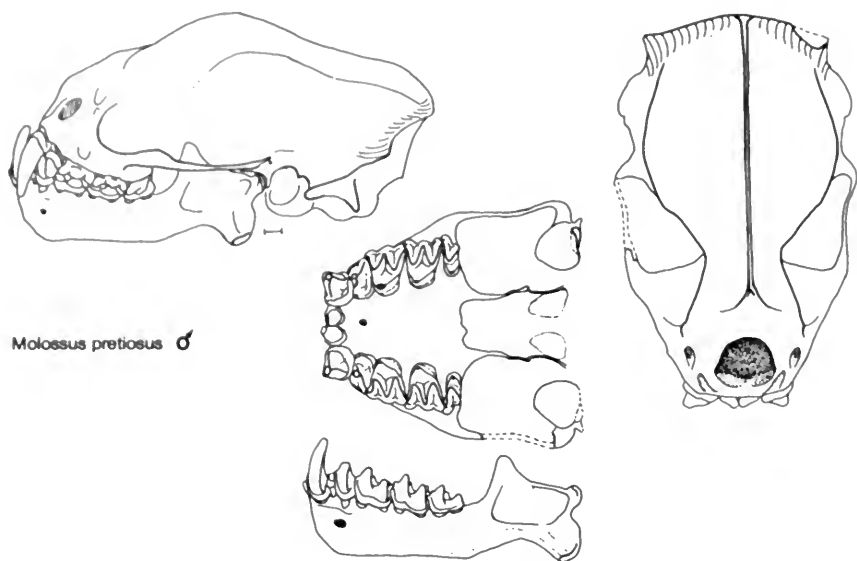


Molossus trinitatus ♂

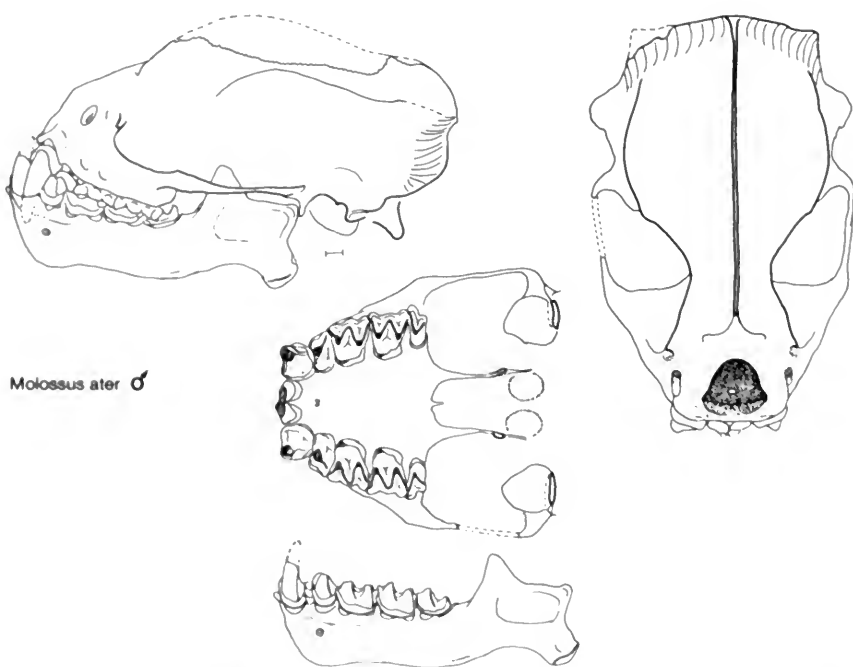


Molossus sinaloae ♂

FIGURE 9.



Molossus pretiosus ♂



Molossus ater ♂

FIG. 9. Seven species of *Molossus* arranged from small to large. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandible are given for each.

Morphologically, the species of *Molossus* are among the most derived molossids in the sense that they have lost teeth due to the foreshortening of the jaw. More qualitative distinguishing features include an upper tooththrow of broad molariform teeth with shearing edges and an upper intercanine space, not emarginate as in several other genera, but filled with two sturdy beaklike incisors. Upper tooththrows of *M. ater* and *Tadarida macrotis*, bats of approximately the same size (maxillary tooththrows = 7.9 and 8.4 mm, respectively; whereas MTR/GSL = 36.7 and 36.5 per cent) are illustrated in Figure 5. Proportionally and actually, the canines and molars of *M. ater* are much larger than those of *T. macrotis*, the latter having retained a rather large PM³ (table 3).

It seems ecologically reasonable that *Molossus* is capable of eating hard items such as beetles, and that it can fly very fast. Food studies done thus far support the first prediction of eating hard prey. Howell & Burch (1974) reported a large percentage by volume of beetle remains in *M. molossus* in Costa Rica (100 per cent in one and 88 per cent in eight of nine specimens) and a substantial percentage of non-moth remains in *M. ater* (50 per cent mixed Hymenoptera, Coleoptera, and Orthoptera in one specimen). Pine (1969) reported much the same in another specimen of *M. ater* with 86 per cent Hymenoptera (2–8 mm long and mostly ants) and 12 per cent Coleoptera (8–25 mm long). My own analysis of fecal samples of five Central American species of *Molossus* shows the feces to have few moth scales compared with the numbers found in some species of *Tadarida* (table 9). The samples examined have a large proportion of beetle exoskeleton in them, and only two of 15 of the small *M. coibensis* had more than a few thousand moth scales in them. Anecdotally, the strength with which a large *Molossus* can bite was communicated to me by Scott Altenbach, who said it gave him one of the worst bites he had ever suffered from a bat and that, by comparison, the bite of *T. macrotis* was mild.

Species of *Molossus* are probably fast fliers, but are capable of less maneuverable flight because their narrow wing tips would have less camber and less lift. Attempts to launch and fly the large *M. ater* in a 17-m flight chamber have proved unsuccessful (Altenbach, personal communication). Several molossid species need an elevated place to drop from to get enough lift to fly. Little quantitative and comparative flight data among molossid species have been collected, and what data that have are difficult to compare because of differing techniques from study to study. Struhsaker (1961) calculated a higher aspect ratio in *Tadarida brasiliensis* rather than in *Molossus nigricans* (= *M. ater*). This could mean that *T. brasiliensis* is the faster flier, if higher aspect ratio does indicate faster flight as Vaughan (1959, 1966) suggests; but *T. brasiliensis* flies easily in an enclosed room and can even take off from the floor. This species of *Tadarida* is also a smaller, lighter bat. The relative length of the last phalanx of digit IV is longer in *T. brasiliensis* (12.67 per cent) than in *M. ater* (4.84 per cent). Observations of where various species of *Molossus* fly support the fast flight idea. McNab (1971) mentioned that *M. molossus* flies above the canopy, and Fenton (1972) noted that *M. ater* and several other molossids were caught only in the upper levels of the canopy. Lawlor (1973, p. 76) reported that two species of *Molossus*, *M. ater*, and *M. bondae*, "fly only in areas of little obstruction, commonly above the tree canopy, as they feed upon insects," and D.C. Carter (personal communication) has netted *Molossus* either over deep pools or streams

TABLE 7. Nearest of most highly correlated neighbors of each bat from size-in distance, size-out distance, and the correlation matrices. At least two neighbors are given for each bat, but three are given for species of *Eumops* and species in the Conglomerate (*Molossops*, etc.). A small distance value or a large correlation value indicates a high degree of phenetic similarity between two bats.

| | <u>Tadarida</u> | | | <u>Chaerephon</u> | | |
|-----------|--------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|--------------------------------|
| | Distance size-in | Distance size-out | Correlation | Distance size-in | Distance size-out | Correlation |
| T AEGYPTA | E BONARA .608 TC ALOYA .618 | T BRASIA .393 TR KALIN .459 | T TENIOA .694 T BRASIA .645 | TC BIVIA .366 T ANSORA .505 | T ANSORA .337 TC RUSSA .357 | TC RUSSA .660 T ANSORA .624 |
| T AFRICA | T FULMIN .681 T LOBATA .715 | T FULMIN .453 T LOBATA .555 | T AUSTRA .775 T AUSTRA .630 | TC BENMI .438 TC MAJOR .467 | TC BIVIA .381 TC MAJOR .450 | TC BIVIA .620 TC CHAPI .591 |
| T ANSORA | TC RUSSA .355 TC NIGEA .372 | TC BIVIA .256 TC ALOYA .337 | TC BIVIA .778 TC RUSSA .722 | TC ALOYA .366 T ANSORA .394 | T ANSORA .256 TC NIGEA .348 | T ANSORA .778 TC RUSSA .665 |
| T AURISA | T FEMORA .528 T LATICA .615 | T FEMORA .420 T LATICA .425 | T FEMORA .882 T MACROA .785 | TC CHAPI .587 TR PLANA .600 | TC BIVIA .397 TC MAJOR .410 | TC MAJOR .645 TC NIGEA .644 |
| T AUSTRA | T TENIOA .530 T KUBORI .637 | T TENIOA .518 T BRASIA .588 | T TENIOA .814 T KUBORI .687 | TC JOBEN .511 TC CONDA .516 | TC TREFVO .493 TC PLICA .510 | TC CONDA .517 TR SANSA .503 |
| T BRASIA | TR PLANA .560 TR KALIN .578 | T AEGYPTA .393 TR KALIN .468 | T AEGYPTA .645 TR KALIN .613 | TC BENMI .505 TC MAJOR .513 | TC CHAPI .440 TC MAJOR .468 | TC BENMI .569 TC CHAPI .549 |
| T FEMORA | T AURISA .528 T LATICA .557 | T AURISA .420 T MACROA .508 | T AURISA .883 T MACROA .780 | TC FUMIA .412 TC NIGEA .425 | TC BIVIA .363 TC NIGEA .375 | TC CHAPI .645 TC NIGEA .612 |
| T FULMIN | T LOBATA .436 T TENIOA .605 | T LOBATA .432 T AFRICA .453 | T LOBATA .809 T AFRICA .775 | T ANSORA .372 TC RUSSA .401 | TC BIVIA .348 T ANSORA .367 | TC RUSSA .664 T ANSORA .652 |
| T KUBORI | T FULMIN .635 T AUSTRA .637 | T BRASIA .578 T AUSTRA .602 | T AUSTRA .687 T TENIOA .555 | TC ANSORA .419 TC BIVIA .482 | TC BIVIA .406 TC FUMIA .411 | TC FUMIA .593 T ANSORA .501 |
| T LATICA | T FEMORA .557 T ANSORA .565 | T AURISA .425 TC ALOYA .523 | T AURISA .682 T FEMORA .598 | TC MAJOR .412 T ANSORA .445 | TC BIVIA .355 T ANSORA .386 | TC CHAPI .632 T ANSORA .581 |
| T LOBATA | T FULMIN .436 T TENIOA .638 | T FULMIN .432 T AFRICA .555 | T FULMIN .809 T AFRICA .725 | TC ANSORA .355 TC NIGEA .401 | T ANSORA .355 TC ALOYA .357 | T ANSORA .722 TC NIGEA .664 |
| T MACROA | T AURISA .613 T TENIOA .650 | T FEMORA .508 T AURISA .526 | OTO MARA .799 T AURISA .785 | | | |
| T TENIOA | T AUSTRA .530 T FULMIN .605 | T AUSTRA .518 T AEGYPTA .521 | T AUSTRA .814 T FULMIN .713 | | | |

TABLE 7. Continued.

| MODS | | NORMOPTERUS - SAUROMYX - PLATYMOPS | | | |
|----------|----------|------------------------------------|----------------------|---------------|---------------|
| | | Distance size-in | Distance size-out | Correlation | |
| TM BRACH | TM THERA | .335 | TM THERA .335 | TM THERA .837 | TR ACETA |
| | TM LEONA | .557 | TM TREVO .413 | TM NANUA .735 | TR MINUA .467 |
| TM CONDA | TC JOBEN | .516 | TM DEMOA .490 | TM DEMOA .570 | TR KALIN .491 |
| | TM NIVEI | .523 | TM CONGA .492 | TC JOBEN .517 | TR BECCR |
| TM CONGA | TM TREVO | .526 | TM DEMOA .391 | TM MIDAA .690 | TR JUGUA |
| | TM NIANG | .605 | TM SANSA .445 | TM TREVO .637 | TR NOEFA .483 |
| TM DEMOA | TM NIVEI | .451 | TM NIVEI .351 | TM NIVEI .710 | TR PHRUD .518 |
| | TM SANSA | .522 | TM MIDAA .362 | TM SANSA .587 | TR KALIN .764 |
| TM LEONA | TM THERA | .516 | TM NANUA .394 | XIPHONYC .841 | TR NOEFA .400 |
| | TM BRACH | .557 | XIPHONYC .402 | TM NANUA .829 | TR NOEFA .471 |
| TM MIDAA | TM CONGA | .615 | TM DEMOA .362 | TM CONGA .690 | TR PHRUD .796 |
| | TM TREVO | .851 | TM NIVEI .374 | TM TREVO .536 | TR MINUA .780 |
| TM MOPSA | TM DEMOA | .407 | TM SANSA .397 | TM SANSA .750 | TR PLANA .408 |
| | TM NIANG | .550 | TM NANUA .480 | TM LEONA .521 | TR PLANA .775 |
| TM NANUA | XIPHONYC | .497 | TM LEONA .394 | TM LEONA .829 | TR LORIA .880 |
| | TM LEONA | .585 | TM BRACH .445 | XIPHONYC .793 | TR LORIA .796 |
| TM NIANG | TM TREVO | .424 | TM TREVO .417 | TM TREVO .691 | TR MINUA .292 |
| | TM CONGA | .605 | TM NIVEI .468 | TM CONGA .595 | TR KALIN .336 |
| TM NIVEI | TM DEMOA | .451 | TM DEMOA .351 | TM DEMOA .710 | TR NOEFA .295 |
| | TC JOBEN | .511 | TM TREVO .378 | TM TREVO .573 | TR MINUA .292 |
| TM SANSA | TM MOPSA | .407 | TM MOPSA .397 | TM MOPSA .750 | TR KALIN .336 |
| | TM DEMOA | .522 | TM CONGA .445 | XIPHONYC .604 | TR NOEFA .296 |
| TM TREVO | TM NIANG | .424 | TM THERA .374 | TM NIANG .691 | TR KALIN .460 |
| | TM CONGA | .526 | TM NIVEI .378 | TM CONGA .637 | TR MINUA .435 |
| TM THERA | TM BRACH | .335 | TM BRACH .335 | TM BRACH .837 | TR NOEFA .448 |
| | TM LEONA | .516 | TM TREVO .374 | XIPHONYC .721 | TR PLANA .475 |
| XIPHONYC | TM NANUA | .497 | TM LEONA .402 | TM LEONA .841 | SAUROMYX .724 |
| | TM LEONA | .613 | TM NIVEI .472 | TM NANUA .793 | TR ACETA .673 |
| | | | | | TR MINUA .682 |

TABLE 7. Continued.

Molossops - Macrotalotyropus - Synomops - Myotis - ChiropteraEurope

| | Distance size-in | Distance size-out | Correlation | | Distance size-in | Distance size-out | Correlation |
|-----------|---------------------|----------------------|----------------|-----------|---------------------|----------------------|---------------|
| MP TEMMA | NEOPLATA .492 | NEOPLATA .491 | NEOPLATA .744 | E AURIPA | E GLAUC .584 | M BONDAA .523 | E GLAUC .714 |
| | TR LORIA .575 | CP PLANA .518 | TR LORIA .652 | | TM NIANG .658 | M SINALA .566 | E UNDERA .597 |
| | CP PLANA .587 | TR MINUA .563 | CP PLANA .644 | | TM CONGA .660 | E GLAUC .578 | M ATERA .596 |
| NEOPLATA | MP TEMMA .492 | MP TEMMA .491 | MP TEMMA .744 | E BONARA | TC NIGEA .548 | E UNDERA .476 | E PEROTA .542 |
| | TR MINUA .560 | TR MINUA .534 | TR MINUA .624 | | TC BIVIA .578 | TR MINUA .529 | T LOBATA .481 |
| | TR LORIA .611 | E UNDERA .550 | PLATTHOP .596 | | TC ALOYA .585 | TR PLANA .585 | T AFRICA .448 |
| CP BRACA | TM NIVEI .727 | CP PLANA .303 | CP GREZZA .693 | E GLAUC | E AURIPA .584 | E MAURIS .499 | E UNDERA .736 |
| | PRO CEN .784 | CP GREZZA .382 | C PARVID .635 | | T AFRICA .760 | E UNDERA .566 | E AURIPA .714 |
| | M ATERA .788 | MP TEMMA .594 | CP PLANA .599 | | E MAURIS .790 | E AURIPA .578 | E MAURIS .663 |
| CP GREZZA | CP PLANA .410 | CP PLANA .306 | CP PLANA .797 | E HANISAA | E BONARA .743 | E BONARA .690 | T AURISA .353 |
| | MYOP WHA .615 | CP BRACA .381 | CP BRACA .693 | | TC MAJOR .755 | T AURISA .739 | E BONARA .302 |
| | TC MAJOR .623 | TR MINUA .592 | M BONDAA .451 | | T AURISA .805 | TC MAJOR .750 | T PEMORA .302 |
| CP PLANA | CP GREZZA .410 | CP BRACA .303 | CP GREZZA .797 | E MAURIS | E BONARA .662 | E GLAUC .499 | E GLAUC .663 |
| | MYOP WHA .587 | CP GREZZA .306 | MP TEMMA .644 | | TC ALOYA .669 | E UNDERA .605 | E AURIPA .547 |
| | MYOP WHA .629 | MP TEMMA .518 | CP BRACA .599 | | TC BIVIA .672 | E BONARA .620 | E UNDERA .443 |
| MYOP ALB | TM NIANG .757 | MYOP WHA .528 | C PARVID .501 | E PEROTA | E UNDERA .800 | E BONARA .702 | E UNDERA .795 |
| | M ATERA .817 | MP TEMMA .666 | MYOP WHA .474 | | TC AFRICA 1.195 | T LOBATA .737 | OTO HANA .706 |
| | TM TREVO .845 | NEOPLATA .700 | CP BRACA .465 | | TM HIDA 1.225 | T PEROTA .753 | T AFRICA .661 |
| MYOP WHA | CP GREZZA .615 | MYOP ALB .528 | MP TEMMA .566 | E UNDERA | E PEROTA .800 | E BONARA .476 | E PEROTA .795 |
| | CP PLANA .623 | MP TEMMA .578 | M COIBEA .491 | | TM HIDA .889 | TR MINUA .538 | E GLAUC .736 |
| | M COIBEA .721 | TR MINUA .595 | E UNDERA .597 | | T AFRICA .982 | NEOPLATA .550 | T AFRICA .674 |
| C PARVID | C TORQUIT .301 | C TORQUIT .278 | C TORQUIT .982 | | | | |
| | E UNDERA 1.510 | MP TEMMA .862 | CP BRACA .635 | | | | |
| | E PEROTA 1.882 | TR LORIA .899 | E UNDERA .597 | | | | |
| C TORQUIT | C PARVID .301 | C PARVID .278 | C PARVID .982 | | | | |
| | E UNDERA 1.493 | CP BRACA .627 | CP BRACA .627 | | | | |
| | E PEROTA 1.888 | TR JUGUA .943 | E UNDERA .547 | | | | |

TABLE 7. Continued.

| Molossus | | | | Otocorys - Promops - Vespertilionids | | | |
|-----------|---------------------------------|--------------------------------|---------------------------------|--------------------------------------|--------------------------------|--------------------------------|--------------------------------|
| | Distance size-in | Distance size-out | Correlation | | Distance size-in | Distance size-out | Correlation |
| M ATERA | M PRETIA .536 M SINALA .619 | M SINALA .312 M BONDAA .317 | M SINALA .851 M PRETIA .813 | OTO MARA | OTO WROA .574 T TENIOA .775 | OTO WROA .412 OTO SECA .557 | OTO WROA .928 T MACROA .799 |
| M BONDAA | M MOLOSS .360 M SINALA .406 | M COIBEIA .251 M ATERA .317 | M COIBEIA .919 M MOLOSS .900 | OTO PAPU | OTO SECA .513 TC PLICA .729 | OTO SECA .497 OTO WROA .555 | OTO SECA .819 OTO WROA .704 |
| M COIBEIA | M MOLOSS .439 M BONDAA .446 | M BONDAA .251 M MOLOSS .375 | M BONDA .919 M MOLOSS .871 | OTO SECA | OTO PAPU .513 OTO WROA .742 | OTO WROA .327 OTO PAPU .497 | OTO WROA .903 TO PAPU .819 |
| M MOLOSS | M BONDAA .360 M COIBEIA .439 | M SINALA .293 M BONDAA .332 | M BONDAA .900 M SINALA .895 | OTO WROA | OTO MARA .574 T TENIOA .680 | OTO SECA .327 OTO MARA .412 | OTO MARA .928 OTO SECA .903 |
| M PRETIA | M ATERA .536 M SINALA .607 | M ATERA .477 M SINALA .532 | M ATERA .813 M SINALA .765 | PRO CENA | PRO NASU .559 M SINALA .646 | PRO NASU .313 M TRINIT .510 | PRO NASU .818 M SINALA .540 |
| M SINALA | M BONDAA .406 M MOLOSS .450 | M MOLOSS .293 M ATERA .312 | M MOLOSS .895 M BONDAA .856 | PRO NASU | PRO CENA .559 M TRINIT .596 | PRO CENA .313 M TRINIT .595 | PRO CENA .818 M SINALA .573 |
| M TRINIT | M BONDAA .425 M SINALA .465 | M BONDAA .423 M SINALA .434 | M SINALA .802 M BONDAA .792 | | | | |
| | | | | MIMETILL | TR PHRID .858 | NYCTALUS .765 | TR PHRID .597 |
| | | | | NYCTALUS | T AEGYPA .833 | MIMETILL .765 | MIMETILL .534 |

TABLE 9. Moth scale counts from fecal samples of various molossid species (method modified after Black, 1974).

| Species | Scales/gram | Remarks | Species | Scales/gram | Remarks |
|---------------------------|-------------|---|------------------------------|-------------|-----------------------------|
| <u>Molossus ater</u> | 0 | | <u>Molossus sinaloa</u> | 1,257 | |
| <u>Molossus ater</u> | 542 | Non-moth leg | <u>Molossus sinaloa</u> | 1,359 | Beetle parts, seeds? |
| <u>Molossus ater</u> | 870 | | <u>Molossus sinaloa</u> | 1,360 | |
| <u>Molossus ater</u> | 2,250 | Beetle parts (legs, antennae, or mouth parts) | <u>Molossus sinaloa</u> | 4,188 | Beetle parts?, Lepidopteran |
| <u>Molossus bondae</u> | 222 | | <u>Molossus greenhalli</u> | 0 | Beetle parts? |
| <u>Molossus bondae</u> | 762 | | | | |
| <u>Molossus colbensis</u> | 0 | Beetle parts | <u>Tadarida brasiliensis</u> | 1,702 | |
| <u>Molossus colbensis</u> | 0 | Beetle exoskeleton | <u>Tadarida brasiliensis</u> | 1,823 | |
| <u>Molossus colbensis</u> | 0 | Beetle mandible | <u>Tadarida brasiliensis</u> | 2,452 | |
| <u>Molossus colbensis</u> | 0 | | <u>Tadarida brasiliensis</u> | 3,196 | Non-moth, Dipteran parts |
| <u>Molossus colbensis</u> | 0 | | <u>Tadarida brasiliensis</u> | 119,596 | Moth parts, Dipteran? |
| <u>Molossus colbensis</u> | 0 | | | | |
| <u>Molossus colbensis</u> | 0 | | <u>Tadarida macrotis</u> | 16,726 | |
| <u>Molossus colbensis</u> | 119 | Beetle part, Hymenopteran? | <u>Tadarida macrotis</u> | 33,929 | Moth parts |
| <u>Molossus colbensis</u> | 1,231 | Dipteran?, Hymenopteran? | <u>Tadarida macrotis</u> | 138,648 | |
| <u>Molossus colbensis</u> | 1,515 | | <u>Tadarida macrotis</u> | 144,032 | Moth parts |
| <u>Molossus colbensis</u> | 1,525 | | | | |
| <u>Molossus colbensis</u> | 1,818 | | | | |
| <u>Molossus colbensis</u> | 2,045 | | | | |
| <u>Molossus colbensis</u> | 2,525 | | | | |
| <u>Molossus colbensis</u> | 17,973 | | | | |
| <u>Molossus colbensis</u> | 23,333 | | | | |
| <u>Molossus pretiosus</u> | 0 | Beetle parts | | | |
| <u>Molossus pretiosus</u> | 62 | Beetle parts | | | |
| <u>Molossus pretiosus</u> | 260 | Beetle parts | | | |
| <u>Molossus pretiosus</u> | 2,203 | | | | |
| <u>Molossus sinaloa</u> | 75 | Beetle parts, seeds? | | | |
| <u>Molossus sinaloa</u> | 897 | | | | |

or on forest roads and paths. No species of *Molossus* seem to roost in caves; rather, they are found in small colonies under palm leaves, in hollow trees, under roofs, in sheds and attics, in crevices of cliffs, and under bridges.

Promops

Promops consists of two Neotropical species, *P. centralis* and *P. nasutus*, which are difficult to distinguish from some species of *Eumops* on the PCA (fig. 4). *Promops* is very *Molossus*-like, but is slightly less robust in jaw proportions (mean relative dentary thickness is 12 per cent, see table 6) and in development of sagittal and lambdoidal crests. Like *Molossus*, *Promops* has ears neither joined by a band over the nose nor completely separated, moderately deep basi-sphenoid pits, lips without wrinkles, narrow-tipped wings, and V-shaped M³s. Unlike *Molossus*, *Promops* bears a vestigial PM³ (fig. 10).

Nearest neighbor distances and correlation place the two species of *Promops* closest to one another, but the next nearest neighbors are members of *Molossus*, particularly *M. trinitatus* (size-out distance, table 7). The latter is a species of *Molossus* of slightly less robust build than other species of the genus, and its similarity to *Promops* is substantiated by its positioning on the PCA plots (fig. 4). Besides *Molossus*, *Promops* has near neighbors among species of *Eumops*, particularly *E. glaucinus*, *E. maurus*, and *E. underwoodi*. These neighbors are closer than *Molossops* or species of *Cynomops*.

The intrageneric distance, size-out, is 0.313, a compact average third only to that of *Cheiromeles* and *Cynomops* (table 5). The size-in average is large, 0.559, a reflection of the size difference between the two species.

Among genera, *Promops* averages 0.687 in size-out distance from *Molossus*, 0.704 from *Molossops*, and 0.775 from *Cynomops* (table 8). It is farthest from *Cheiromeles* at 1.260.

The larger *Promops centralis* (GSL = 20.0 mm) is about the size of *Molossus pretiosus*, and the smaller *Promops nasutus* (GSL = 17.7 mm) is about the size of *M. molossus* or *M. bondae*. Like *Molossus*, both species of *Promops* are very similar in shape to each other.

Ecologically, species of *Promops* are probably like those in *Molossus* in that they have the same narrow-tipped wings, but they may take foods that are not as hard because they have slightly less robust jaws and skulls. Food and flight data are nonexistent. Species of *Promops* have been found under bark in the tops of trees (Brosset, 1966), obtained from hollow trees (Jones, 1966), and captured over a shallow pond surrounded by pine-oak forest (LaVal, 1969).

Mops

Species of *Mops* lie to the lower left of *Molossus* on the PCA plots (fig. 4). OTU's included in the cluster of *Mops* are: *M. brachyptera*, *M. condylura*, *M. congica*, *M. demonstrator*, *M. leonis*, *M. midas*, *M. mops*, *M. nanula*, *M. niangarae*, *M. niveiventer*, *M. sarasinorum*, *M. trevori*, *M. thersites*, *Xiphonycteris spurrelli*, and one species of *Chaerephon*, *C. jobensis*. These bats are found mostly in Africa, but a few species occur in the Indo-Australian region. *Mops* is presently regarded as a subgenus of *Tadarida*, but in my study they form a distinct group fairly distant from *Tadarida*. *Xiphonycteris spurrelli* has been considered a genus (Rosevear, 1965; Hayman & Hill, 1971), but here it clusters with species of *Mops*.

As suggested by the placement on axis II and also axis III, dentaries of species of *Mops* are slightly less robust than those in *Molossus* (mean relative dentary

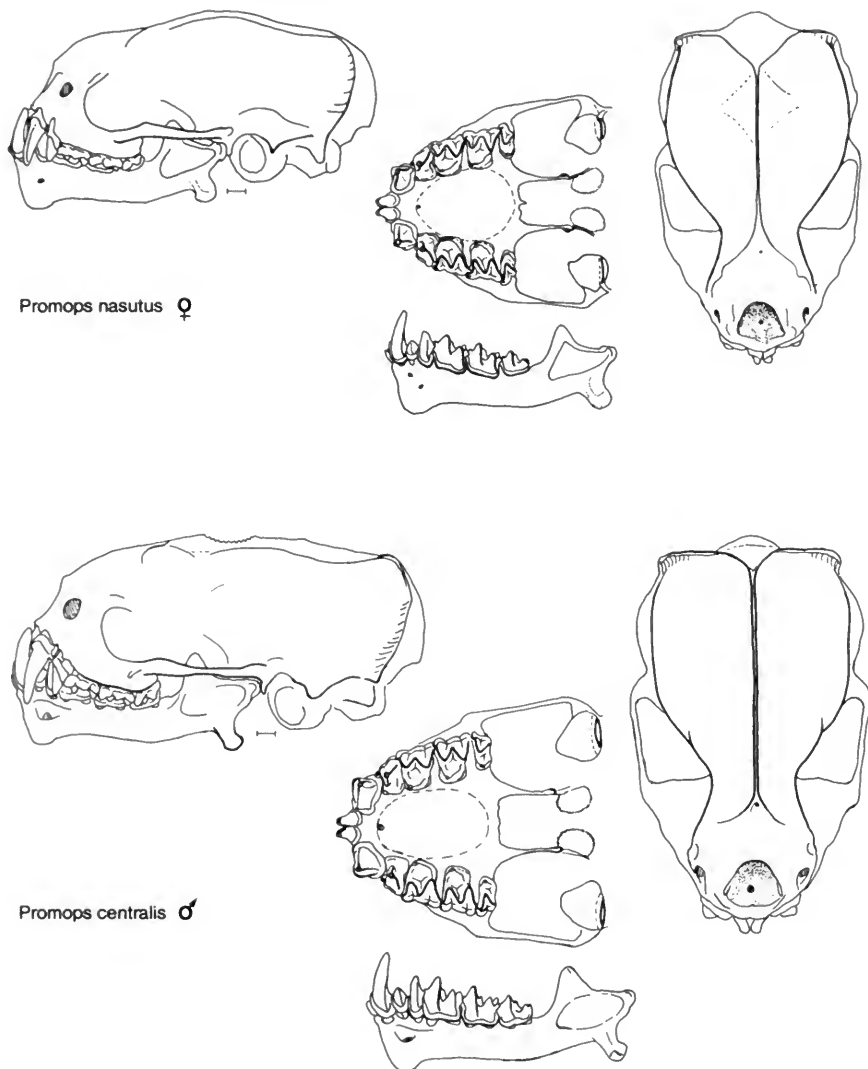
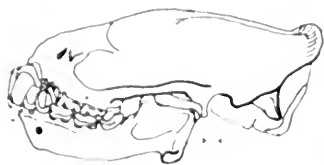


FIG. 10. Two species of *Promops*. Lateral, dorsal, and palatal views of the skull and lateral view of the mandible are given for both.

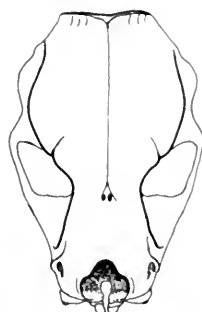
thickness is 13.2 per cent) as are other jaw proportions except height of the mandibular condyle above the toothrow (table 6). Species of *Mops* do not have the extreme sagittal crest development of that in *Molossus* nor is the posterior commissure on the third upper molar completely lost (except in *Mops mops* and *M. sarasinorum*, both Indo-Australian species). The third upper premolar shows variable states, from absent in *M. mops* to poorly developed in most of the African forms, and large in *Xiphonycteris* (fig. 11). Ears of species of *Mops* are joined over the nose with a band, basisphenoid pits vary from shallow to deep, and the lips are very wrinkled (appendix A).



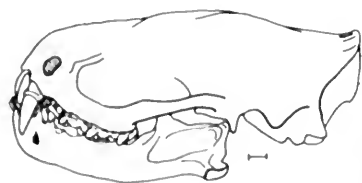
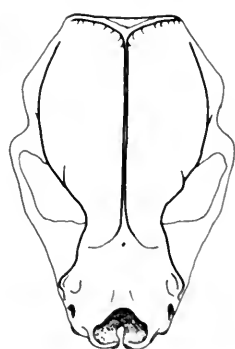
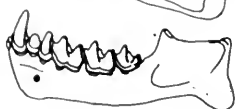
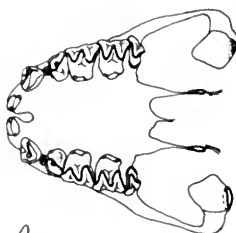
Mops spurrelli ♂



Mops nanula ♂



Mops leonis ♀



Mops brachyptera ♀

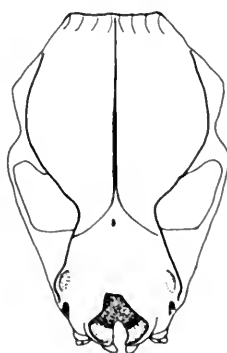
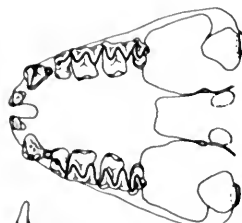
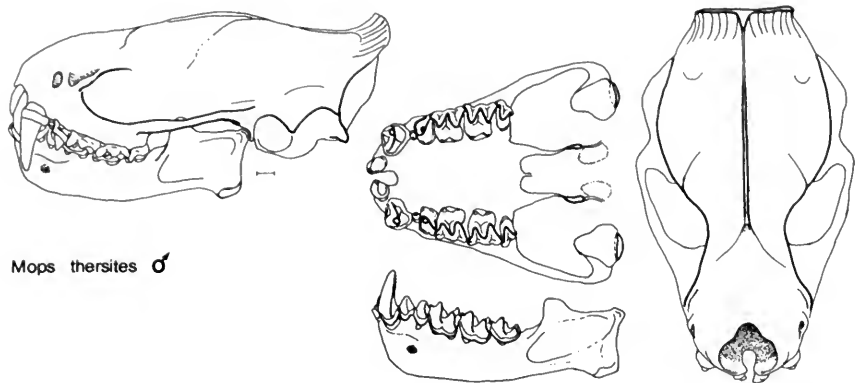
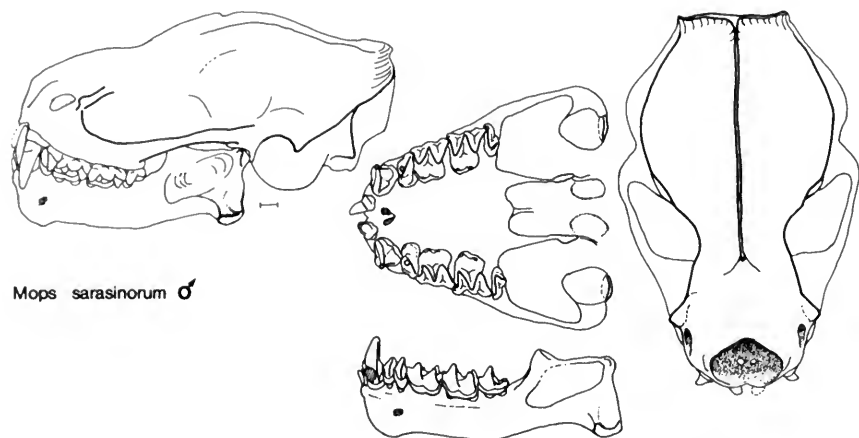


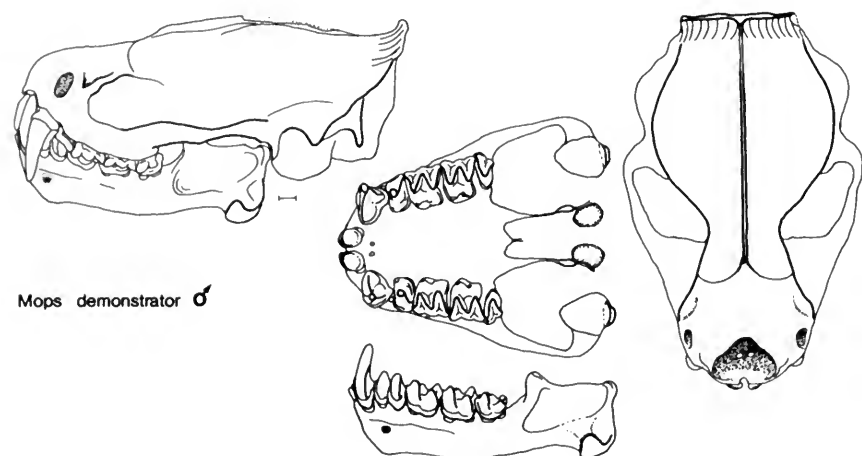
FIGURE 11.



Mops thersites ♂

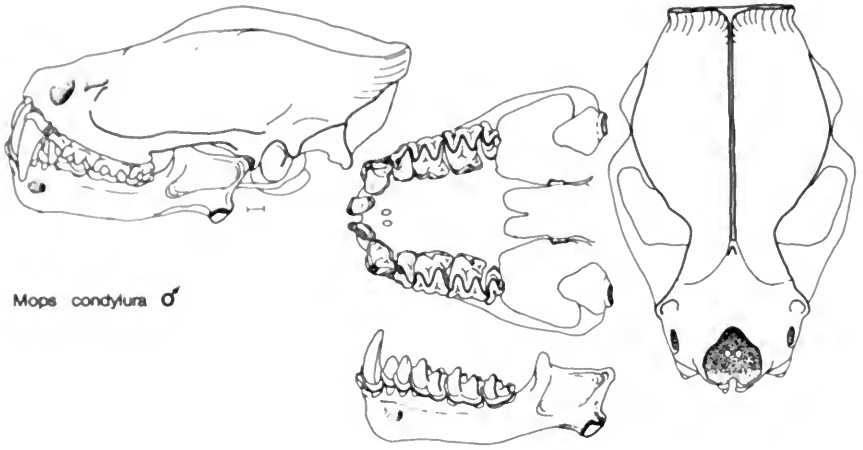


Mops sarasinorum ♂

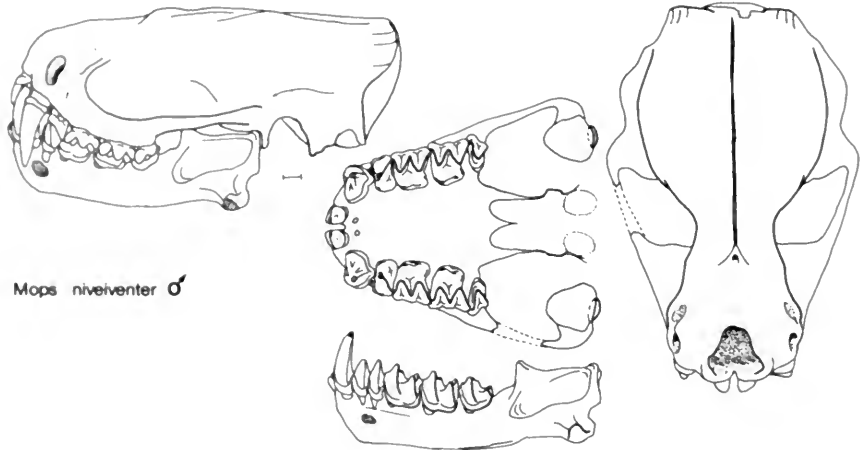


Mops demonstrator ♂

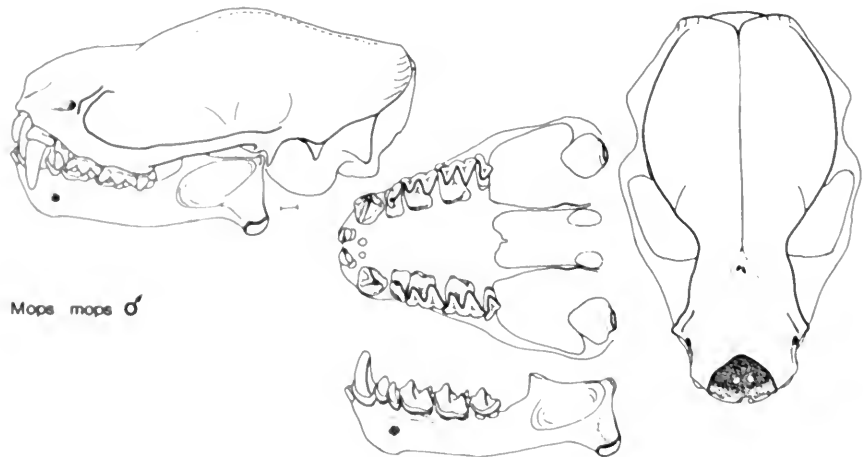
FIGURE 11.



Mops condylura ♂



Mops niveiventer ♂



Mops mops ♂

FIGURE 11.

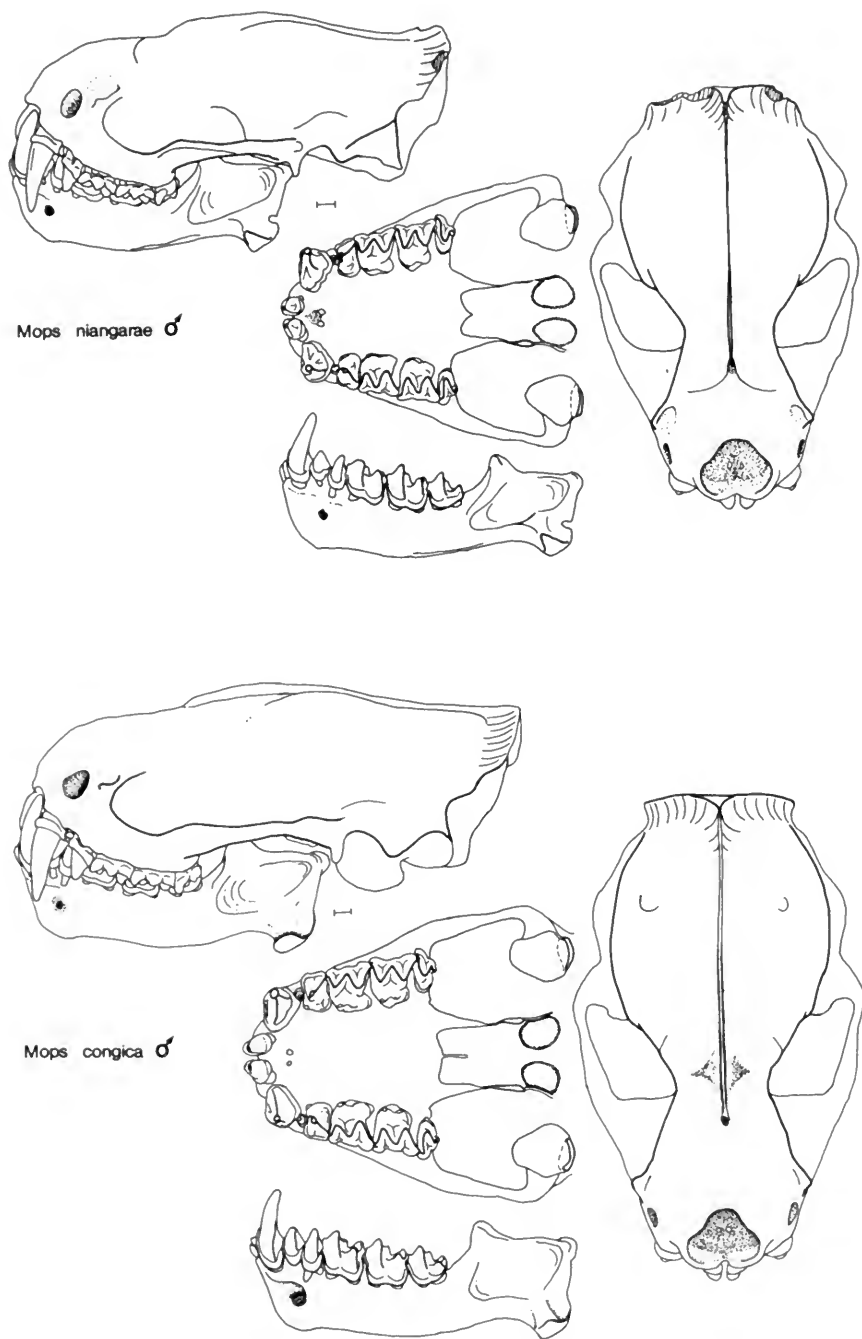


FIGURE 11.

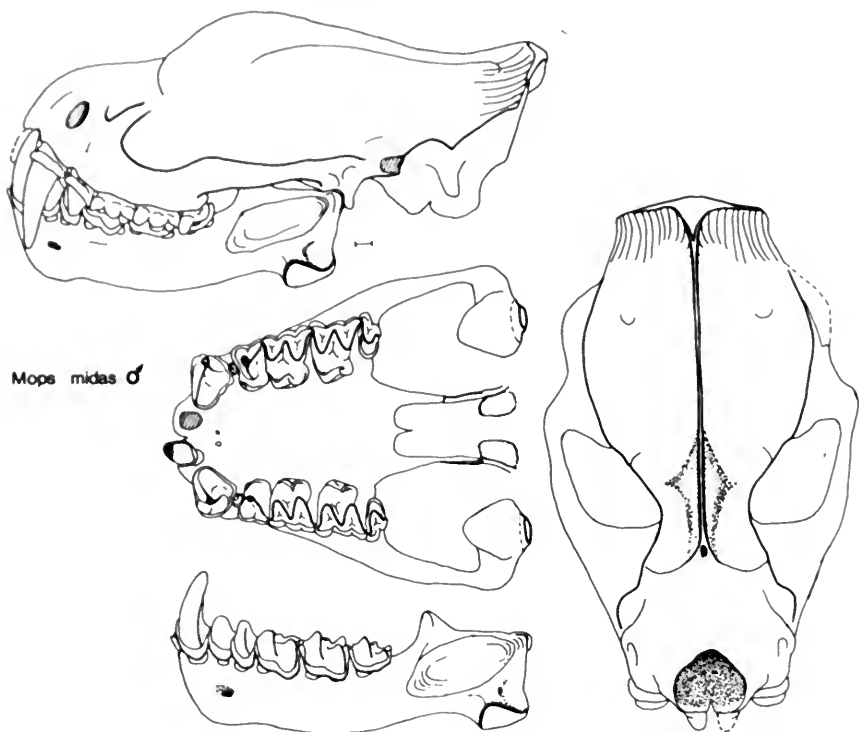


FIG. 11. Thirteen species of *Mops* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for all 13.

Characters that distinguish species of *Mops* from species of *Molossus* on axis IV are broad wing tips (mean of relative length of second phalanx of digit IV is 16.2 per cent), little development of the lateral lambdoidal crest (although great development of superior lambdoidal), many wrinkles, and large ears. The two clusters, *Mops* and *Molossus*, are opposites on this axis.

Species of *Mops* are distinctly separate from species of Old World *Tadarida* and *Chaerephon* because of the relatively shorter M^3 (posterior ridge reduced) and better developed sagittal and lambdoidal crests. Although there is some morphological overlap with *Tadarida* and more with *Chaerephon*, species of *Mops* on the average have thicker dentaries, higher coronoid processes, more elevated condyles, and greater moment arm indices of the jaw muscles (table 6).

Xiphonycteris and *Chaerephon jobensis* are included in the cluster of species of *Mops* on the PCA. These two bats have characteristics similar to those of *Mops*, namely, thick jaws and many of the related jaw proportions and codes (table 6, appendix A). Even when the qualitative multistate characters (codes) are removed from the PCA, these two species cluster with species of *Mops*.

Clustering techniques confirm the impression given by the PCA. With one exception all nearest neighbors in distance (size-in and size-out) are members of *Mops* and all highest positively correlated neighbors are species of *Mops* as

well (table 7). *Xiphonycteris* is closest either to *Mops nanula* or *M. leonis*, all three of which are members of what Koopman (1975) referred to as *Tadarida* (*Xiphonycteris*). In the size-in analysis, the nearest neighbor of *Mops condylura* is *Chaerephon jobensis*. The closest neighbors of *C. jobensis* in the clustering methods are species of *Mops* (table 7).

Average least distance within the taxa both with size excluded and size included is relatively low (table 5). Size-out average of 0.385 is below the dividing point between compact and dispersed groups, and the size-in average is 0.458, also below the average in the size-in matrix. (These figures include *Xiphonycteris* but not *Chaerephon jobensis*.) Average least distance (size-out) among genera in Table 8 shows *Chaerephon* the closest (0.673) to *Mops* and *Cheiromeles* and *Otomops* the farthest (1.178 and 1.152) from *Mops*.

Though individual codes of shape are not as uniform for *Mops* as for *Molossus*, the species look much alike but are of different sizes (fig. 11). The range of sizes in this group is greater than in *Molossus* and, indeed, greater than in any other genus in the study (from 14.9 mm GSL in *Xiphonycteris* and 15.0 mm in *Mops nanula* to 27.0 mm in *M. midas*, see table 1).

I judge the functional capabilities of the jaws in *Mops* to be much like those of *Molossus*, though the jaws and skull are slightly less robust in build. The average relative height of condyle above the toothrow for *Mops* is greater than that in *Molossus* and may give some greater mechanical advantage to make up for a slightly less robust skull. Wings in species of *Mops* are among the broadest-tipped of any of the taxa. The camber produced by the long second phalanx is probably considerable and allows for more maneuverability and possibly slower flight than in *Molossus*. Perhaps species of *Mops* are capable of eating hard-bodied prey as do *Molossus*, but species of *Mops* may not fly like species of *Molossus*. Although little evidence is available for the first contention, Verschuren (1957) reported that stomachs of *Mops condylura* contained legs of *Coleoptera*. Lang & Chapin (1917, p. 491) noted that, "The heavy skull of *Mops (Allomops) osborni* [= *M. condylura*] (Fig. 12, pg. 470), with an enormous sagittal and lambdoid crest, is capable of giving strong support to large muscles of mastication. They are needed to operate the broad grinding, cutting surfaces of the short dental rows. The food of all such Molossidae consists chiefly of hard-shelled insects." Recently, Whitaker & Mumford (1978) reported that nine *Tadarida condylura* (= *Mops condylura*) had consumed 65 per cent Coleoptera, 20.6 per cent Hemiptera, and 11.7 per cent Lepidoptera. Anecdotally, Randolph Peterson told me that *condylura* had a particularly strong bite.

Support for the contention that *Mops* is slower and more maneuverable in flight than *Molossus* is not extensive. Several authors call *midas*, *trevori*, *condylura*, and *demonstrator* savannah species and *congica*, *niangarae*, *thersites*, *leonis* and *nanula* and *Xiphonycteris* forest species (Lang & Chapin, 1917; Verschuren, 1957; Rosevear, 1965; Hayman & Hill, 1971). *Mops condylura*, like many species of *Molossus*, has been found in houses and its widespread distribution includes forest and savannah habitats (Rosevear, 1965). Peterson (1972) stated that the larger species of *Mops* did not seem to overlap ecologically and that *congica* is in high forest (following Rosevear's ecological description), *trevori* is at forest edge or in open forest, and *midas* is in savannah or isolated savannah forests. In conclusion, most species of *Mops* seem to live in places with obstacles in them; few are found in strictly open areas.

Chaerephon

A third compact group to the left of *Mops* on the negative side of the jaw axis is mainly comprised of species of *Chaerephon*, a classical subgenus of *Tadarida*, and like *Mops*, mostly African with a few species found in the Indo-Australian region (figs. 4, 12). The species included here are *C. aloysiisabaudiae*, *C. bivittata*, *C. chapini*, *C. bemmellini*, *C. johorensis*, *C. major*, *C. nigeriae*, *C. plicata*, *C. pumila*, *C. russata*, and a species of *Tadarida*, *T. ansorgei*. Corresponding to the placement of the group on axis II, species of *Chaerephon* have a less robust jaw structure and thinner dentaries (mean of relative dentary thickness is 11.0 per cent). Like *Mops*, however, *Chaerephon* has a similar configuration of ears joined by a band over the nose and the same broad-tipped wings (mean of relative length of second phalanx is 16 per cent). *Chaerephon* has less development of sagittal and lambdoidal crests than *Mops*. Height of condyle above the toothrow is less than that in *Mops* but similar to that in *Molossus*. The posterior commissure on M^3 is at least moderately developed in all species except *pumila*. *Chaerephon jobensis* is exceptional for a species of *Chaerephon* in that its sagittal and lambdoidal crests are well developed and its dentary is thick (14 per cent of dentary length). As mentioned in the *Mops* account, this Indo-Australian *Chaerephon* seems to have more similarities with *Mops* than with *Chaerephon*. The important features which distinguish *Chaerephon* from *Mops* and *Tadarida* are listed in Table 6. *Chaerephon* is distinct from the latter by having a more constricted anterior palatal emargination, well-joined ears, broader wing tips, and on the average a more elevated mandibular condyle and greater moment arm index. *Chaerephon* overlaps with *Tadarida* in relative length of M^3 (though this N-shape is less developed in *Chaerephon*), relative dentary thickness, and relative height of coronoid process, and overlaps with *Mops* in wing tip width and several jaw characters.

A species now in *Tadarida*, *T. ansorgei*, is like *Chaerephon* in many jaw characteristics and in coded characteristics (table 5 and appendix A). Although Koopman (1975) placed *ansorgei* along with *Chaerephon bemmellini* and *Chaerephon bivittata* into the subgenus *Tadarida*, I cannot agree with this consignment because of the evidence from the PCA and the clustering techniques which suggest that these three species are members of *Chaerephon*. *Tadarida ansorgei*'s nearest neighbor, size-in, is *Chaerephon nigeriae* at 0.358 (low for size-in) and for size-out is *Chaerephon bivittata* at 0.277. This last distance is so low that one wonders if the two bats may not be members of the same species. The bat with the highest positive correlation with *ansorgei* is also *bivittata*. The three questionable species (*T. ansorgei*, *C. bemmellini*, and *C. bivittata*) are close to other members of *Chaerephon* and not to *Tadarida* (table 7). If one considers *T. ansorgei* a species of *Chaerephon*, then nearly all members of the genus have congeners as nearest neighbors in the three clustering methods. The exception is *jobensis* which is closest to a species of *Mops* in all these analyses. *Chaerephon chapini*, a small bat, is nearest *Mops nanula*, another small bat, in the size-in distance analysis.

Within-taxon average distance (size-out) for *Chaerephon* is on the compact side (0.364, *ansorgei* and *jobensis* included). Nearest neighbors to *Chaerephon* among taxa are, as expected from placement on the PCA, *Mops* at 0.673, *Tadarida* at 0.743, *Mormopterus* at 0.746; and its farthest neighbor is *Cheiromeles* at 1.252 (tables 5, 8).

Body sizes of species of *Chaerephon* are medium and range from a GSL of 16.0 mm in *chapini* to 21.0 mm in *aloyisiabaudiae* and *jobensis*.

Not only do the species of *Chaerephon* have generally less robust jaws and skulls than species of *Mops*, they also have a condyle less elevated above the toothrow (mean relative condylar height is 12.9 per cent versus 14.8 per cent in *Mops*). Degrees of difference in this character are thought to be related to the effectiveness of the bite, but the advantages to the bat are not yet determined. Average dentary thickness for *Chaerephon* is even less if *jobensis* is excluded as a species (reduced mean relative thickness is 9.5 per cent) as are the characteristics moment arm index and relative coronoid height.

Because the species of *Chaerephon* have broad-tipped wings, they are probably slower, more maneuverable flyers among molossids. *Chaerephon* should be less capable than *Mops* of consuming hard prey items because of its thinner dentaries and generally less robust skull.

Few data are at hand about food habits. Allen (1939) mentioned a specimen of *Chaerephon limbatus* (= *C. pumila*) that was found to have eaten adult moths of the cotton bollworm, whereas Verschuren (1957) reported stomachs of *ansorgei* to contain wings of Formicidae, hymenopteran antennae, and coleopteran legs. Whitaker & Mumford (1978) reported that nine specimens of *pumila* had consumed 48.3 per cent Hemiptera, 18.4 per cent Coleoptera, 13.3 per cent Lepidoptera, 10.4 per cent Diptera and unidentified insects, and 8.3 per cent Orthoptera.

Recently, Vestjens & Hall (1977) reported on stomach contents in nine specimens of *Tadarida jobensis*. Eight of the nine had moth remains and three had remains of plant bugs and ants. There also was one occurrence each of ground beetles, water beetles, leaf beetles, unidentified beetles, flies, crickets, and earwigs. I think *jobensis*, with its thick jaws, can probably take anything up to the hardness of beetles.

Support is also weak for the postulated slower, more maneuverable flight of species of *Chaerephon*. Several, such as *russata*, *aloyisiabaudiae*, *bemmelini*, *pumila*, and *nigeriae*, have been found at forest edge or in forest situations (Peterson, 1971b; Fenton & Peterson, 1972; Verschuren, 1957; Rosevear, 1965). Others, however, such as *major*, *ansorgei*, and *chapini*, are considered savannah species (Lang & Chapin, 1917; Verschuren, 1957). *Chaerephon pumila* has been found in both places. Brosset (1966) reported that *plicata* has been found in immense groups in grottos in southern Asia.

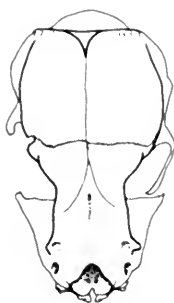
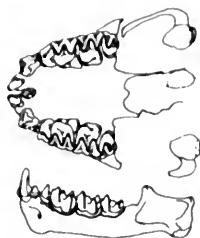
Fenton (1972) divided several African molossids into two groups based on his metacarpal III/metacarpal V ratio. Four species of *Chaerephon* had a higher ratio than four species of *Mops* and were thought to be swifter. His measure did not take into account the phalanges. Based on the analysis in my study, both *Mops* and *Chaerephon* have very similar wing configurations, and I believe that they fly in the same way.

Otomops-Tadarida macrotis

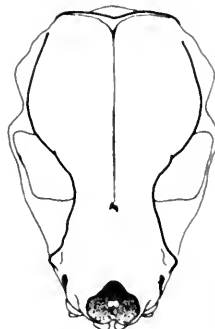
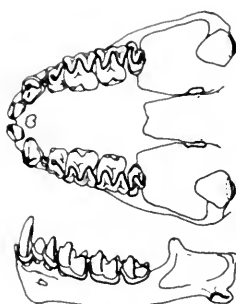
The extreme cluster, opposite *Molossus*, on axis II consists of four bats: three species of *Otomops* (*O. papuensis* excluded) and *Tadarida macrotis* (fig. 4). This phenetically cohesive group occurs over a tremendous geographic area: *O. secundus* occurs in New Guinea, *O. wroughtoni* in India, *O. martiensseni* in Africa; and *T. macrotis* inhabits southwestern United States and much of Central and



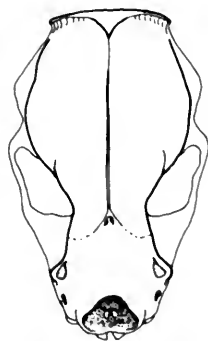
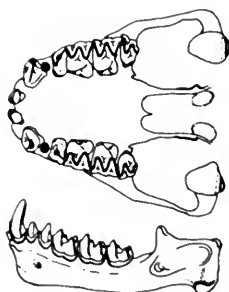
Chaerephon chapini ♂



Chaerephon major ♀



Chaerephon pumila ♂



Chaerephon bemmelini ♂

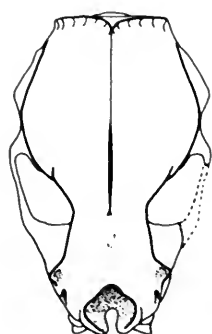
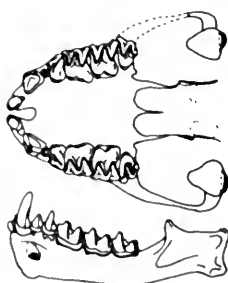
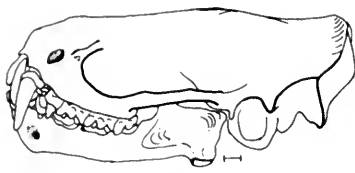
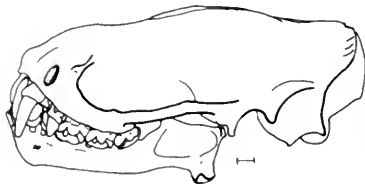
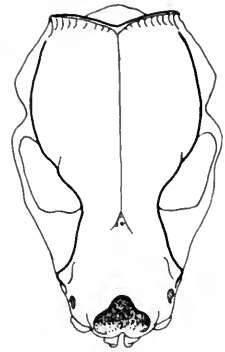
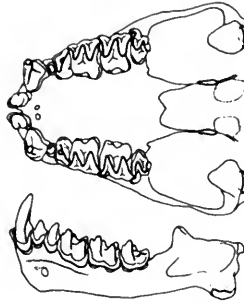


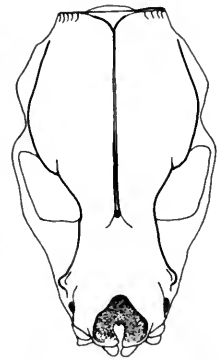
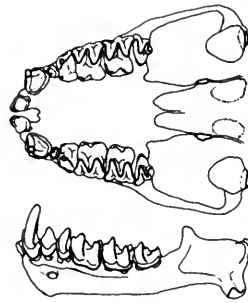
FIGURE 12.



Chaerephon nigeriae ♂



Chaerephon ansorgei ♂



Chaerephon russata ♂

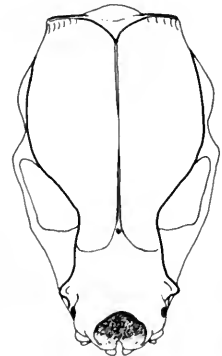
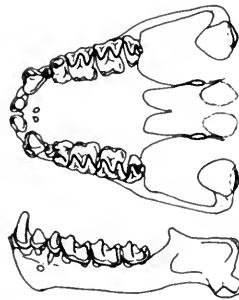
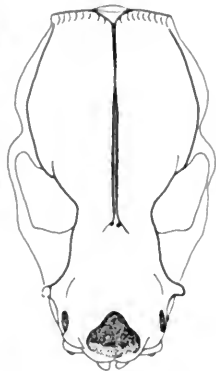
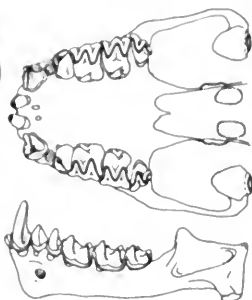


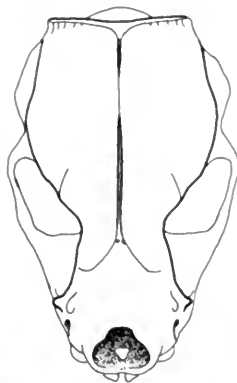
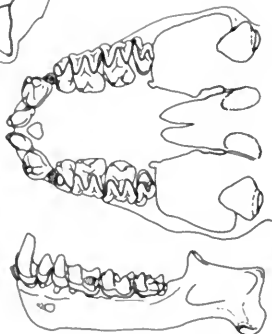
FIGURE 12.



Chaerephon plicata ♂



Chaerephon bivittata ♂



Chaerephon aloysiisabaudiae ♂

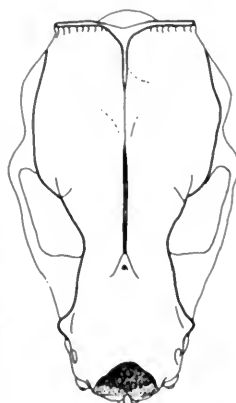
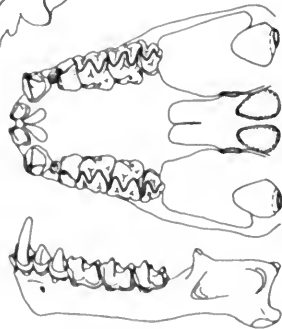


FIGURE 12.

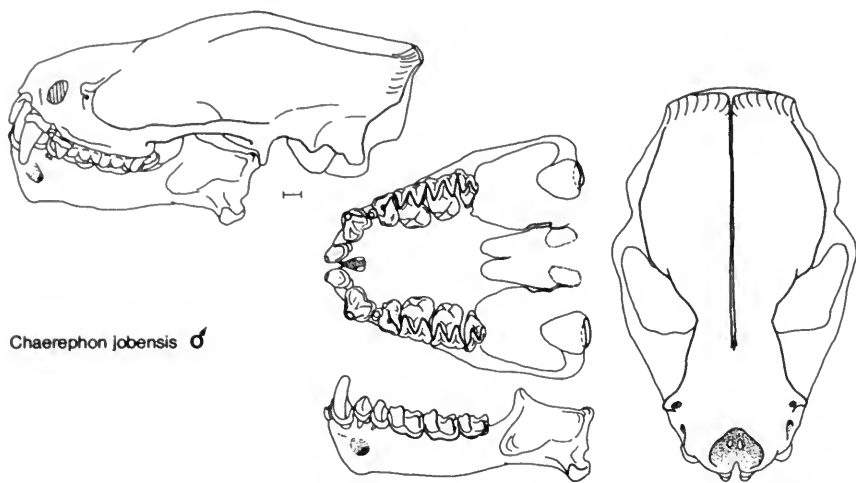


FIG. 12. Eleven species of *Chaerephon* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for all 11.

South America. Characteristic of these bats are their very thin dentaries (mean relative dentary thickness is 9.0 per cent), low coronoid processes, presence of a large premolar well spaced between canine and PM⁴, M³ with full-sized posterior commissure (N-shaped), condyle not so elevated above the toothrow (mean relative condylar height is 6.0 per cent), and only slight development of sagittal and lambdoidal crests. The large ears are joined anteriorly over the nose, basisphenoid pits are very deep, and lips are wrinkled either finely or as deep troughs (table 6, appendix A).

Perhaps the small *Otomops papuensis*, *Eumops perotis*, and *Tadarida teniotis*, OTU's on the periphery of this cluster, should be included (fig. 4), but they do not have all of the extreme characteristics that occur in the *Otomops-T. macrotis* cluster. *Otomops papuensis* has a thicker dentary, and *E. perotis* has an almost V-shaped M³. *Tadarida teniotis* is not as extreme in the joining of the ears, development of the sagittal crest, or depth of the basisphenoid pits.

Only two variables are highly correlated with axis IV, and neither the species of *Otomops* nor *T. macrotis* are extreme in both of them. Although *T. macrotis* has extremely narrow wing tips (relative length of second phalanx is 3.1 per cent), it has only a moderately developed lateral lambdoidal crest, and *Otomops* has only an intermediate wing tip (12.6 per cent) and no development of the crest.

To this point the PCA representation of the bats has corresponded for the most part with the clustering analyses. Although *Otomops* and *T. macrotis* are phenetically similar, the clustering analyses give a slightly different picture. In all three (size-in, size-out, and correlation), species of *Otomops* are closest to each other, including *O. papuensis* and excluding *T. macrotis*. The latter on the other hand is nearest other New World *Tadarida* in the two distance analyses but is most highly correlated with *O. martiensseni*.

Because of the nearest neighbors indicated by the clustering techniques, the summary averages, both within and among, follow generic groupings, placing all species of *Otomops* together and all species of *Tadarida* together. *Otomops'*

within-genus average (size-out), is 0.390, still within the range that I consider compact. The size-in average is 0.535, a number affected by the substantial variation in size among species of *Otomops*. Among genera, the nearest neighbor to *Otomops* is *Tadarida* (0.829) and the farthest neighbor is *Cheiromeles* (1.743). *Otomops* and *Cheiromeles* are the farthest apart of any two groups (tables 5, 8).

Greatest skull lengths of the similarly shaped species of *Otomops* and *Tadarida* *macrotis* are on the large side, at 19.7 mm and 27.2 mm in *O. papuensis* and in *O. martiensseni*, respectively, and at 23.0 mm in *T. macrotis* (table 1, figs. 5, 13).

The slender jaws of these bats are probably capable of a very wide gape because their coronoid processes are low and their mandibular condyle is almost in the same plane as the tooththrow. Because of their jaw structure as well as the slight crest development, I think these bats are less capable of chewing up hard-shelled insects. The bats described in this section probably eat soft-bodied creatures such as moths, perhaps large ones. There is evidence, at least for the New World *T. macrotis*, that not only is there a large quantity of moth material in its feces (table 9), but that it is taking Macrolepidoptera, probably of the family Sphingidae (Ross, 1967). Easterla & Whitaker (1972) reported that in 98.0 per cent of 49 stomachs of *T. macrotis*, large moths made up 86.1 per cent of the volume. In 28.6 per cent of the stomachs, Gryllidae/Tettigoniidae made up 6.7 per cent of the volume, and in 8.2 per cent of the stomachs, Formicidae made up 4.1 per cent of the volume.

There is also qualitative evidence that the narrow wing-tipped *T. macrotis* is a fast flier. Although *macrotis* has been flown successfully in a 17-m enclosed

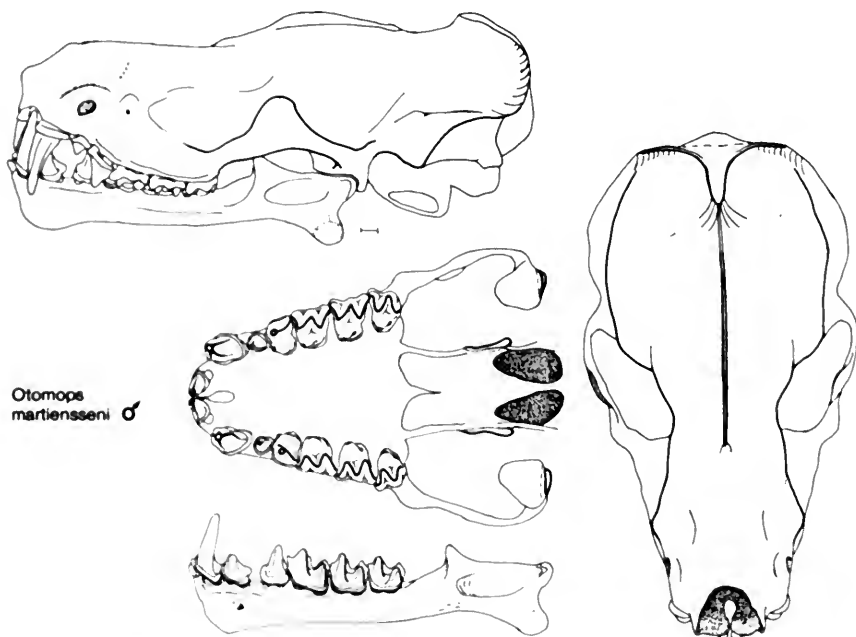


FIG. 13. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Otomops*.

space, it had to be launched by hand and it flew at speeds seemingly slower than those observed outside. Hayward & Davis (1964) think that because *T. macrotis* has such narrow wings it is not found in mines or caves.

There are few data on the food or flight habits of species of *Otomops*. Recently, a large colony of *O. martiensseni* was found roosting in a cave in Kenya (Mutere, 1973), and Brosset (1966) reported a colony of 40 individuals of *O. wroughtoni* in India. Brosset further noted that species of *Otomops* appear to be forest Chiroptera, unlike other molossids, and have extremely powerful flight. If cave roosting and forest-dwelling does require bats to have broader wing tips, the species of *Otomops*, rather than *T. macrotis*, may be suited for such an existence.

Species of *Otomops* and *T. macrotis* have some of the largest ears, relatively, of any molossid (0.549 correlation with axis II, table 2). The ears project forward, and Vaughan (1966) hypothesized that ears of this type may be used as additional airfoils to help keep the head aloft in flight (see also Kingdon, 1974). Also, if a relationship exists between echolocation, large ears, and deep basisphenoid pits, it has not yet been elucidated; but many of these large-eared molossids, specifically *T. macrotis*, *T. femorosacca*, *Eumops perotis*, and *E. underwoodi*, are known to emit loud low-frequency clicks. Schum (1972) has analyzed this click in *T. macrotis* and concluded that this high-intensity, low-frequency sound is most efficient for active, long-distance echoranging. A function of this nature would be appropriate for these fast-flying molossids that may not maneuver as well as bats with broader wings. It is not known whether species of *Otomops* emit these sounds, but they certainly have the same large ears and deep basisphenoid pits, the deepest of any molossid. An interesting description and discussion of the morphology of the basisphenoid pits in *Otomops martiensseni* is presented by Valdivieso et al. (1979). These authors also mention that large ears and deep basisphenoid pits seem to be correlated in molossids.

Tadarida

The bats remaining are not easily grouped by the principal components analysis, but in the distance analyses and in correlation very few species have nearest neighbors outside their genus (table 7). I lump monotypic genera with the taxa to which they are most closely related in the clustering techniques.

Species of *Tadarida* are well scattered along the negative side of axis II (fig. 4). The classical subgenus, which I presently treat as a genus, consists of species in the New World, *T. aurispinosa*, *T. brasiliensis*, *T. femorosacca*, *T. laticaudata*, and *T. macrotis*; species in Africa, *T. aegyptiaca*, and the large *T. africana*, *T. lobata*, and *T. fulminans*; species in Australia and New Guinea, *T. australis* and *T. kuboriensis*; and a species in the Palearctic, *T. teniotis*. It is the most cosmopolitan group thus far discussed and, with the possible exception of *Mormopterus*, is the most widespread genus in the family. With a wide distribution of this sort one might expect the species within the genus to be dissimilar and, hence, dispersed compared to a group that is, for the majority of species, concentrated on one continent.

All the bats on this negative side of axis II have relatively thin dentaries (fig. 4). *Otomops*, of course, has the thinnest but *Tadarida* is nearly as thin (mean relative dentary thickness is 10.0 per cent). Variation within the genus on this axis involves differing jaw proportions of dentary thickness, coronoid height,

moment arms for temporal and masseter, and height of mandibular condyle above the lower toothrow (table 6).

Variation on axis III separates most American *Tadarida* (except *brasiliensis*) from the Old World *Tadarida*. Those species on the negative side of this axis have most or all of the following characters: ears completely joined by a band superior to the rostrum, a moderately developed anterior sagittal crest, a low coronoid process, moderate to deep basisphenoid pits, and a narrow inter-orbital and lacrimal width (appendix A).

Axis IV is determined by another constellation of characters. Any variation caused by the wing characteristic is not apparent. Most New World *Tadarida* have a narrow wing tip (range of relative length of second phalanx is 3.1–4.2 per cent) but are lowered on the axis because of the codes concerning development of lateral lambdoidal crest and ear junction. Two other characteristics important on the negative end and affecting position of the narrow wing-tipped bats are relatively big ears (ear/forearm ratio) and a well developed PM³. *Tadarida kuboriensis* and *T. australis* have broad-tipped wings (relative length of second phalanx 14 per cent and 17 per cent, respectively). *Tadarida africana* is high (more positive) on axis IV because it not only has a narrow wing tip (9 per cent), but it also possesses a well-developed lateral lambdoidal crest. In these last features *africana* approaches the appearance of several species of *Eumops*.

Tadarida teniotis, the only Palearctic *Tadarida*, is in an isolated position on the far negative end of axis II, as extreme as *Otomops* and *T. macrotis*, but it is negative on axis III probably because of its wide interorbital and lacrimal width.

There appear to be groups within the cluster of species of *Tadarida* on the PCA plots that may be expected either on the basis of geographic location or because of body size. The clustering techniques place the New World *Tadarida*, with the exception of *T. brasiliensis*, close to each other (table 7). *Tadarida brasiliensis* is closer to *T. aegyptiaca* in size-out distance and correlation, but with size-in, is closest to a species of *Mormopterus* (both are small bats). A second subgrouping is among *T. africana*, *T. fulminans*, and *T. lobata*, all large African *Tadarida*. The neighbor nearest both *africana* and *lobata* is *fulminans* in all three techniques. One might suspect that the three OTU's represent fewer than three species except that the size-out distance separating them is never less than 0.432, a rather average distance in the more compact groups. Of the species remaining, the African *aegyptiaca* and the New Guinean *kuboriensis* both have different neighbors in the three analyses but both are closest to *brasiliensis* in size-out distance (table 7). *Tadarida teniotis*, found in the Palearctic region, is closest in all three techniques to the Australian *T. australis*.

Average least distance for the genus, size-in, is 0.562 which is affected, I believe, by the substantial amount of variation in the size of the species; and average least distance, size-out, for the genus is 0.458. *Tadarida* is among the dispersed groups (table 5). Among neighboring genera *Tadarida* is nearest the monotypic *Sauromys* (0.711), followed closely by *Chaerephon* (0.743) and then by *Mormopterus* (0.799) and *Otomops* (0.829). The farthest neighbor of *Tadarida* is *Cheiromeles* at a distance of 1.441 (table 8). These neighbors correspond well with the positioning in the principal components analysis (fig. 4).

Greatest skull lengths of *Tadarida* range from 16.5 mm in *brasiliensis* to 24.0 mm in *teniotis* and *africana*. Shapes in the skulls of Old World *Tadarida* do not show predictable change as size increases as do skulls of *Mops* and *Molossus* and, for that matter, New World *Tadarida* (figs. 14, 15).

Because the structure of the jaws in *Tadarida* is much like that of *Chaerephon* and *Otomops*, I suspect that the functional capabilities of the jaws are much the same. *Tadarida* probably concentrates on soft-bodied prey and, indeed, what data there are support this prediction. In the New World species, *brasiliensis*, *femorosacca*, and *macrotis* (see preceding account), a large percentage of their diet consists of moths. *Tadarida femorosacca*, like *macrotis*, is capable of taking Macrolepidoptera (100 per cent in one stomach) but has also taken Microlepidoptera and Coleoptera (85 and 15 per cent, respectively, in one stomach; Ross, 1967). Easterla & Whitaker (1972) reported that in 13 *femorosacca* large moths made up 36.9 per cent of the volume in 69.2 per cent of the stomachs. They also found lesser percentage volume and frequency of many other flying insects (Formicidae as well as Hymenoptera, Hemiptera, Diptera, and Coleoptera) and of unlikely things such as Gryllidae, Tettigoniidae, Cercopidae, and Cicadellidae; all terrestrial insects which were thought to have been captured in the roosts.

Tadarida brasiliensis, a common molossid, has been much studied. Ross (1967) reported this small bat taking prey from 2-10 mm in length and gave the following proportions of food items for 88 specimens: Lepidoptera, 34 per cent; Hymenoptera, 26.2 per cent (flying ants); Coleoptera, 16.8 per cent (scarabs and chrysomelids); Homoptera, 15 per cent; and Hemiptera, 6.4 per cent. A report by Bailey (1931) indicated this species to have taken 95 per cent moths and 5 per cent mixed insects, and Storer (1926) reported over 90 per cent moth material. Sherman (1939) noted that six of eight *Tadarida cynocephala* (= *T. brasiliensis cynocephala*) had eaten Lepidoptera whereas none were found in three vesperilionids (*Lasiurus*, *Dasypterus*, and *Pipistrellus*). He went further to say that two of the eight contained Homoptera; one, Odonata; one, Neuroptera; six, Diptera; four, Coleoptera; and six, Hymenoptera. Ross (1967) mentioned that *brasiliensis* feeds in groups of 10-13 individuals and often prey on densely swarming insects, a foraging method which he calls filter feeding. Vaughan (1966) suggested that such molossids with wrinkled lips fly through the air with their mouths open using their expandable wrinkled lips as a funnel much like the rictal bristles around the mouths of caprimulgidiform birds.

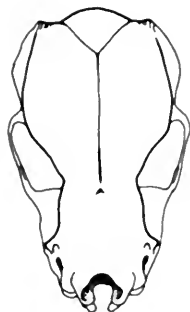
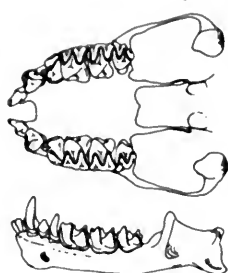
My own data from fecal samples of *T. brasiliensis* show only one sample to have many thousands of moth scales present and four others from a different locality to have only one to three thousand scales (table 9). Some dipteran and other non-moth parts were present. It may be that this bat takes whatever prey species is abundant and because of its small size is capable of taking hard as well as soft items. A similar diversity of prey occurs with *Molossus coibensis* where it seems to be taking soft as well as hard items.

At present there are few food data for the Old World species of *Tadarida*. As mentioned previously *ansorgei*, either a species of *Tadarida* or *Chaerephon*, has been found with remains of Formicidae, other Hymenoptera, and Coleoptera in its stomach (Verschuren, 1957).

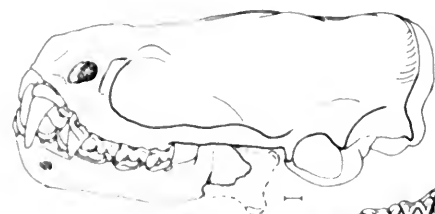
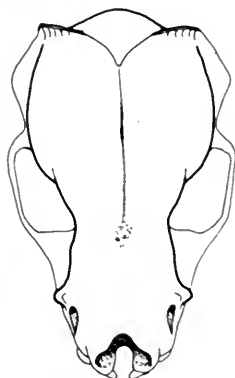
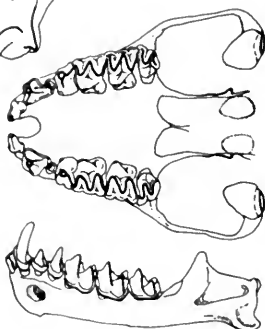
The New World *Tadarida* (except *T. brasiliensis*), with their narrow wing tips, are probably faster and less maneuverable than most of the Old World species. There are no quantitative data on flight in the Old World *Tadarida*, but Findley et al. (1972) estimate speed of flight in some of the New World species based on surface area of the flight membranes and weight of the bats. Those authors project a speed in *brasiliensis* as being 24 m.p.h. and speed in *femorosacca*, *macrotis*, and *Eumops underwoodi* of 27 m.p.h. These were all thought to be



Tadarida brasiliensis ♂



Tadarida aegyptiaca ♂



Tadarida lobata ♀

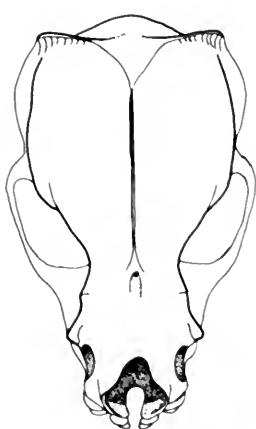
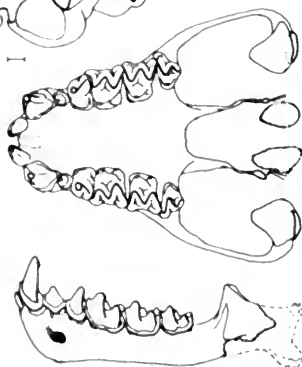
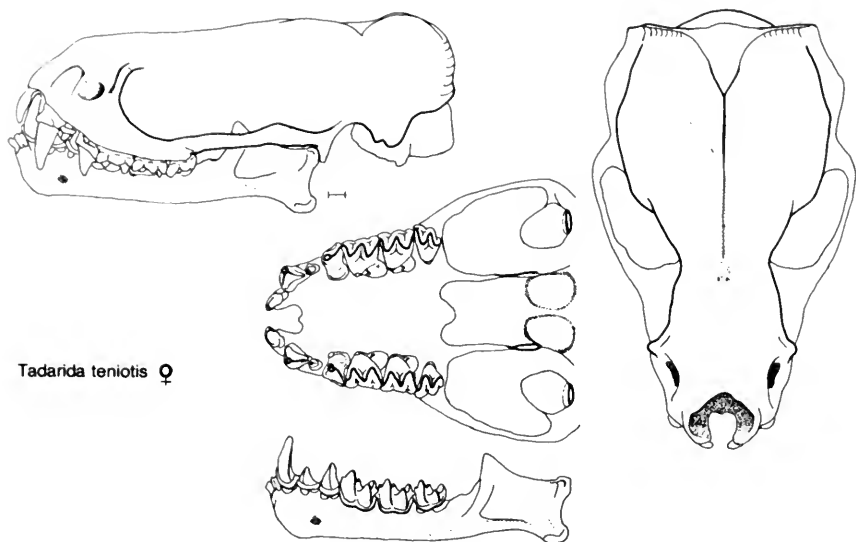
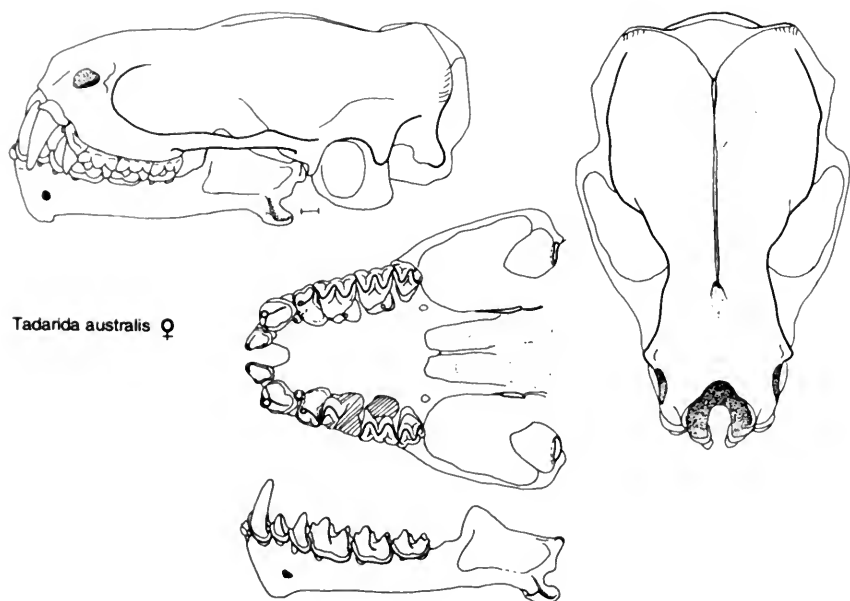


FIGURE 14.



Tadarida teniotis ♀



Tadarida australis ♀

FIGURE 14.

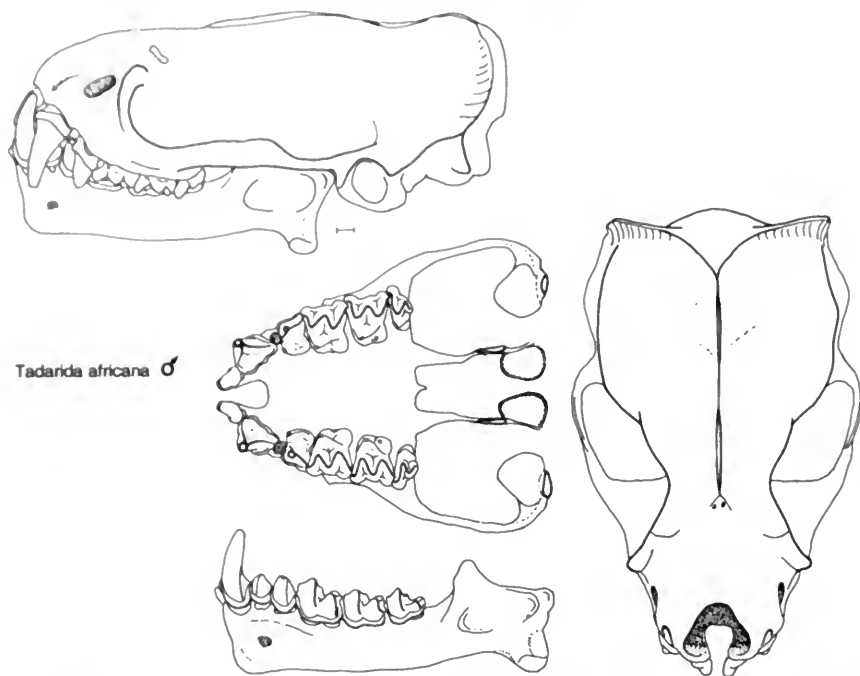


FIG. 14. Six species of *Tadarida* arranged from small to large. Lateral, dorsal, and occlusal view of the skulls and lateral view of the mandibles are given for all six.

underestimates. Allison (1937) calculated a speed of 20 m.p.h. in *brasiliensis*, whereas Hayward & Davis (1964) estimated 10-20 m.p.h. My own observation of *brasiliensis* is that it is not only able to fly in a room with little trouble (it does not crash into walls and can take off from the floor), but it is also very maneuverable. Ross (1967) observed *T. brasiliensis* foraging with the fluttery small pipistrelles. Others have observed that the larger *femorosacca*, *macrotis*, and *Eumops perotis* rarely can take flight in a room and usually crash into a wall if they do (Krutzsch, 1955; Hayward & Davis, 1964). I have successfully launched and seen *macrotis* fly in a 17-m room, although at slow speeds. Vaughan (1966) calculated that *T. brasiliensis* has a lower aspect ratio, and thus slower speed, than *T. macrotis*. A slower speed is supported in this study by the fact that *brasiliensis* has a broader-tipped wing than *macrotis* (table 4).

Tadarida femorosacca and *T. macrotis* are usually found in high places like cliffs and rock crevices, whereas *T. brasiliensis* is found in those places as well as in caves and more enclosed areas (such as roofs of houses). Two of the three, along with a large species of *Eumops*, may be found in the same crevice, but the smaller bats stay in narrow peripheral portions and the larger ones in wide central portions (Krutzsch, 1955). *Tadarida aurispinosa* has been taken in the Bogota Savannah (Tamsitt et al., 1964) and *T. laticaudata* has been taken from a palm 13 m high (Silva-Taboada & Koopman, 1964) and from man-made structures in the lowlands of Guatemala (Jones, 1966). Koopman (personal communication) has seen a large colony of *T. laticaudata europis* in a church in the province of Rondonia in Brazil.

There are few data on the habits of African or Australasian molossids or even on the Palearctic *T. teniotis*; however, some information exists on roosting places of these bats and places of capture. The three large *Tadarida* in Africa are thought to live in cliffs or high rocky places, situations where *T. lobata* and *T. fulminans* have been found. The latter two seem to prefer arid or semi-arid plains (Peterson, 1974). Little is known about *africana* but it has, along with *fulminans*, the narrowest wing tips of the Old World *Tadarida* (relative length of second phalanx is 9.0 per cent). *Tadarida aegyptiaca* has been found in caves and in large buildings (Rosevear, 1965), under stone slabs on a hillside, along with *Sauromys* (Irwin & Donnelly, 1962); and inhabits arid regions in East Africa (Brosset, 1963). The Australasian *kuboriensis* and *australis* have the broadest wing tips in the genus. The former has been found at 2,750 m in *Nothofagus* and moss forest (McKean & Calaby, 1968), and the latter frequents open places where it has been caught in windmill blades some 12 m off the ground (Hall & Richards, 1972). Dwyer (1965) noted that *australis* can launch itself from a rough horizontal surface with great difficulty but cannot maintain flight in a room 7.6 by 4.6 m.

Recently, Vestjens & Hall (1977) reported on the stomach contents of 21 specimens of *Tadarida australis*. There were 20 occurrences of moths, two of scarabs, one of ants, two of unidentified Hymenoptera, and one of unidentified Hemiptera. No remains of water beetles were found as Shortridge (1936) had suspected, but there was a dominance of moth remains.

Bats on the negative end of axis II tend to have larger ears (fig. 4). A few bats on this end also have a loud click which may be related to long-distance echolocation (Schum, 1972). Krutzsch (1944) noted a high-pitched, sharp call in *T. femorosacca*, whereas Peterson (1974) reported that *T. lobata* emits a distinctive single or double-noted loud squeak. Perhaps significantly, all these large-eared, loud-clicking bats (*T. macrotis*, *T. femorosacca*, *T. lobata*, *E. underwoodi*, and *E. perotis californicus*) have deep basisphenoid pits, are found in arid regions, and are considered cliff dwellers.

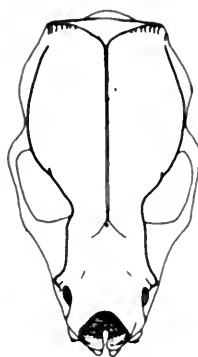
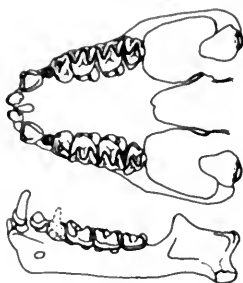
Mormopterus-Sauromys-Platymops

The fourth and last classical subgenus of *Tadarida* is *Mormopterus*, the species of which are scattered but are generally located in the middle of axis II in the PCA plots (fig. 4). *Mormopterus*, like *Tadarida*, is found on several continents: *M. kalinowskii* and *M. phrudus* are from Peru, and *M. minutus* is from Cuba; *M. jugularis* and *M. acetabulosus* are from Africa and Madagascar; and *M. beccarii*, *M. lorae*, *M. norfolkensis*, and *M. planiceps* are from the Australia-New Guinea area. These last three may be taxonomically confused. If the monotypic African genera *Sauromys* and *Platymops* are added to this group, the dispersion is only slightly greater (table 5). Both ordination and clustering procedures indicate a relationship between these two monotypic genera and *Mormopterus*.

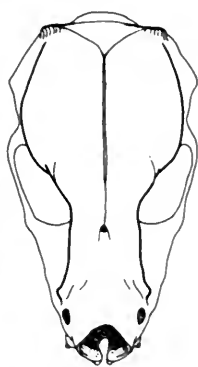
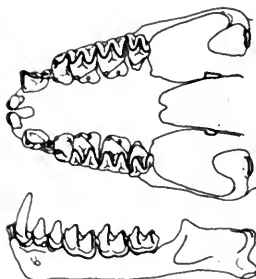
Most variation occurring in these bats is along axis II or the jaw axis. Average relative dentary thickness is about 11 per cent (range from 9.3-14.5 per cent), a mean similar to that of *Chaerephon*. Average height of mandibular condyle is higher than that in any group except *Cheiromeles* (mean relative condylar height is 15.6 per cent, *Sauromys* is less here). All have a well-developed posterior commissure on M³, but few retain PM³ (if present it is usually small); a combination which is somewhat unusual in that the two traits are usually present or absent together (table 6, appendix A). *Mormopterus beccarii* is extreme in all of



Nyctinomops laticaudata ♂



Nyctinomops femorosacca ♂



Nyctinomops aurispinosa ♂

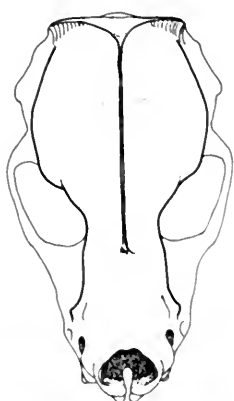
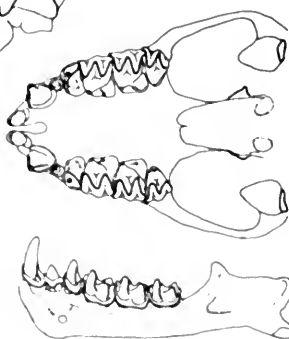


FIGURE 15.

the characters highly correlated with this second principal component. It has a very thick dentary, very high coronoid and condyloid processes, and the largest relative temporal and masseter muscle moment arm index. This bat is also the largest of the group, making it an extreme not only in shape but also in size (fig. 16).

The positions of these bats on the two other axes, III and IV, are not as strikingly variable (fig. 4). As a group, *Mormopterus*, *Platymops*, and *Sauromys* have widely separated small ears (less so for *Sauromys*), shallow or nonexistent basisphenoid pits, little or no wrinkling on the lips, no development of the anterior sagittal crest, a high coronoid process, and a wide face (interorbital and lacrimal breadths). These are all characters which position the group as one of the most positive on axis III. On axis IV variation among the first five or six pertinent characters is such that the bats tend to be grouped around the mid-point of the axis. One interesting occurrence is that *beccarii* has unusually large ears that perhaps causes it to occupy a negative position on this axis. The bats have a relatively broad wing with mean relative length of second phalanx of 15.0 per cent and range from 9.4-18.8 per cent. *Mormopterus phrudus* and *Sauromys* have narrowest wing tips; and *Platymops* and the three Australian *Mormopterus* have the broadest wing tips.

The clustering techniques reveal that all nearest neighbors or highly positively correlated neighbors are within the genus and, as mentioned earlier, nearest neighbors of *Sauromys* and *Platymops* are species of *Mormopterus* (table 7). *Platymops* is nearest *Sauromys* only in the size-in analysis. In both shape analyses *Platymops* is closest to *Mormopterus acetabulosus* in distance (0.673, a substantially great distance, to be sure) and in correlation (0.622). The neighbor, *acetabulosus*, is found on Mauritius and in southeastern Sudan and is sympatric with *Platymops* in southwestern Ethiopia. The South African *Sauromys*, on the

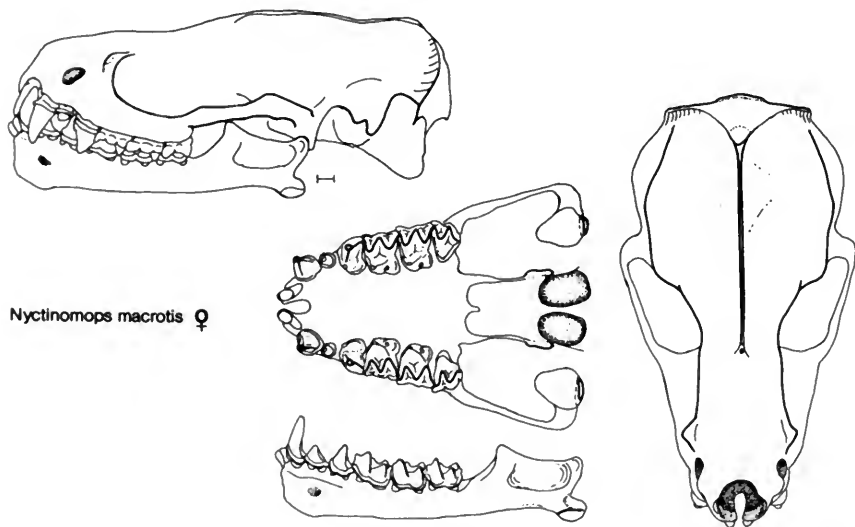
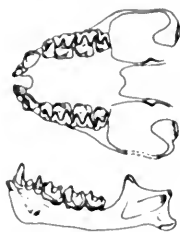


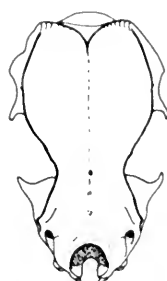
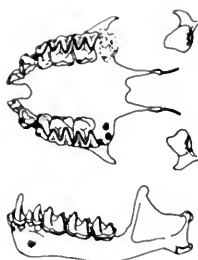
FIG. 15. Four species of *Nyctinomops* (New World *Tadarida*). Lateral, dorsal, and occlusal view of the skulls and lateral view of the mandible are given for all four. Use of the name *Nyctinomops* (Miller, 1902) is explained in the Evolutionary Relationships section.



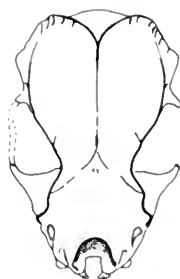
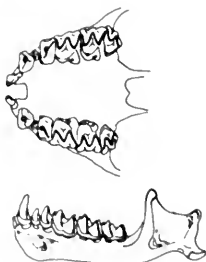
Mormopterus (Mormopterus) minutus ♂



Mormopterus (Mormopterus) lorae ♂



Mormopterus (Mormopterus) norfolkensis ♀



Mormopterus (Mormopterus) kalinowskii ♂

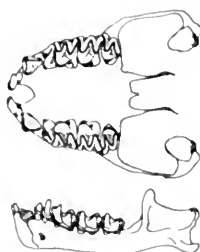
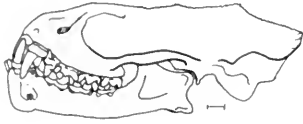
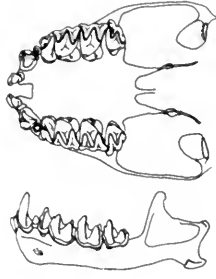


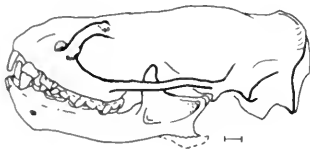
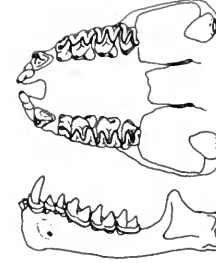
FIGURE 16.



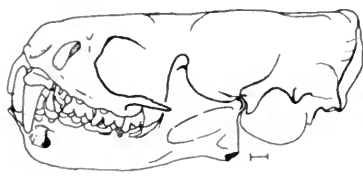
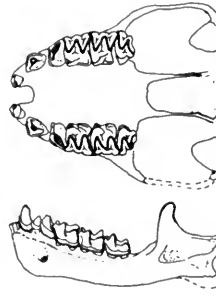
Mormopterus (Mormopterus) planiceps ♀



Mormopterus (Mormopterus) phrudus ♂



Mormopterus (Mormopterus) jugularis ♀



Mormopterus (Mormopterus) beccarii ♂

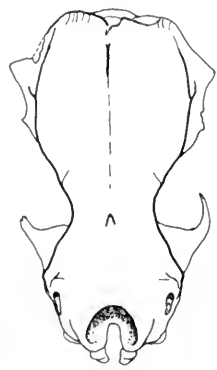
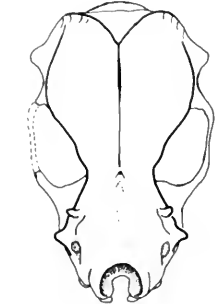
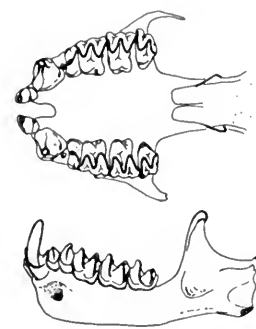


FIGURE 16.

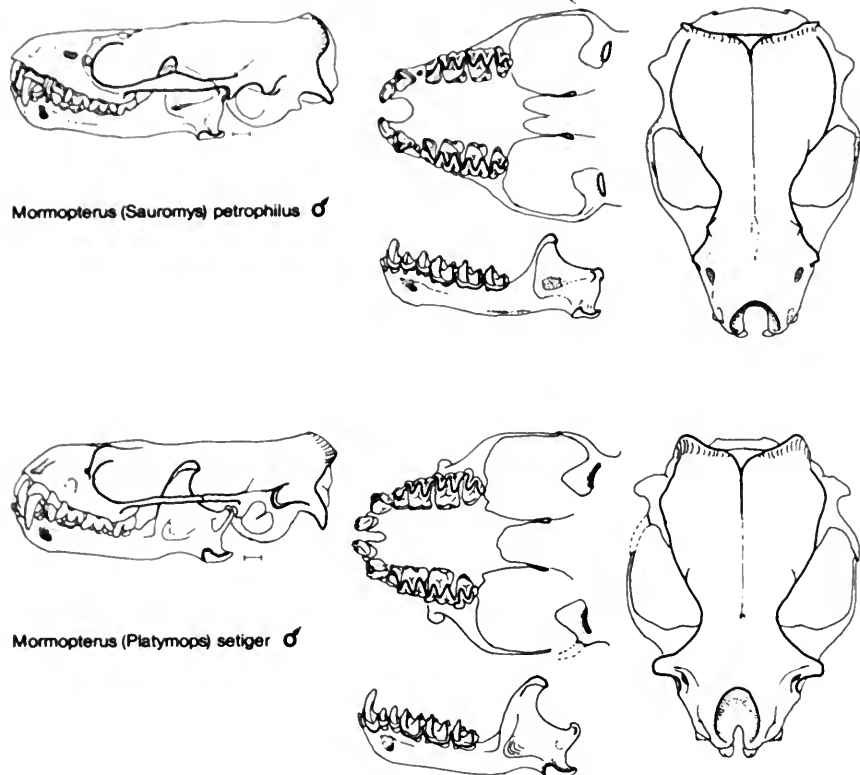


FIG. 16. Ten species of *Mormopterus*, including *Sauromys* and *Platymops*. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandibles are given for each species. The treatment of *Sauromys* and *Platymops* as subgenera is explained in the Evolutionary Relationships section.

other hand, is closest in all three analyses to *Mormopterus norfolkensis* (size-in distance of 0.570, size-out distance of 0.448, and correlation of 0.663), a bat found many miles away on the Cape York Peninsula in Australia.

Within *Mormopterus* the New World representatives are nearly always closest to each other. Only in the correlation analysis is *minutus* most highly correlated with *norfolkensis*. These New World species, *kalinowskii*, *minutus*, and *phrudus*, form a compact group among themselves with size-out distances of less than 0.340. The Australian *Mormopterus* form another tightly bound group in which *loriae*, *norfolkensis*, and *planiceps* are nearest neighbors to one another in all three clustering methods and have no greater size-out distance among them than 0.400. I suspect there may actually be fewer than three species involved in each of these two compact groups of *Mormopterus*, because each has a pair of bats joined at a size-out distance of less than 0.300, a small distance in this analysis.

Mormopterus beccarii from New Guinea and the Moluccas is a distinctive bat in both size and shape and like *Sauromys* and *Platymops* is somewhat distant from other *Mormopterus* species. It is nearest in distance to *jugularis* from

Madagascar (size-in of 0.658 and size-out of 0.595) as well as being most highly correlated with it (correlation of 0.701). *Mormopterus jugularis*, on the other hand, is nearest the Australian *norfolkensis* in both distances but most correlated with the Neotropical *phrudus*. The other Malagasy (and African) *Mormopterus*, *acetabulosus*, is nearest New World species *minutus* in both distances and *kalinowskii* in correlation only.

Though dispersed in the PCA, species of *Mormopterus*, even including the outlying genera, *Platymops* and *Sauromys*, fall on the compact side of least averages within taxa both in size-out and size-in distance (table 5). Nearest neighbors among genera to *Mormopterus* alone are *Sauromys* (0.570), *Molossops* (0.706), and *Neoplatymops* (0.721); farthest are *Otomops* at 1.100 and *Cheiromeles* at 1.023. *Sauromys* is closest to *Mormopterus* (0.570), then to *Tadarida* and *Platymops* (0.711), and farthest from *Cheiromeles* (1.154); *Platymops* is closest to *Neoplatymops* (0.700), *Sauromys* (0.711), *Molossops* (0.737), and *Mormopterus* (0.752) and farthest from *Otomops* at 1.290 (table 8).

Bats of this group are small in size for molossids. Greatest skull lengths range from 13.4 mm in *minutus* to 18.4 mm in *beccarii* including *Platymops* (15.5 mm) and *Sauromys* (17.6 mm, table 1). All species of *Mormopterus* have a similar appearance in that they all possess a delicately shaped and tall coronoid process. The two flat-headed bats *Sauromys* and *Platymops* are similar in this regard (fig. 16). Height of the coronoid may be related to different leverage for the temporal muscle, making the direction of pull directly posteriad rather than posterio-dorsad. This change in temporal muscle force occurs in shrews to an advanced degree and is thought to cause the shift in contact from the superior condylar facet to the inferior condylar facet (Fearnhead et al., 1955). If all the bats in this group are considered flat-headed (to a lesser or greater degree), then the increased height in the coronoid process would compensate in leverage for a temporal muscle that has been forced to extend laterally. The greatest development of the lateral lambdoidal crest is in the African flat-headed bats, *Platymops* and *Sauromys* (also *M. jugularis*), whereas most of the other *Mormopterus* bear a crest only moderately developed. Flat-headedness occurs in several molossids and is thought to be a result of living in very narrow crevices (Peterson, 1965). All of the so called flat-headed bats, *Sauromys*, *Platymops*, and *Neoplatymops*, are phenetically related to *Mormopterus*. Not only is the coronoid process high in these bats, but the mandibular condyle is well elevated above the toothrow. I think this last feature gives some undetermined advantage to the jaw action, an advantage which could be very helpful for small bats with relatively thin dentaries.

Of all molossids, bats of the genus *Mormopterus* are the least known because there are few specimens of species in this genus and little has been written about them. Specimens of *Platymops* and *Sauromys* may be slightly better represented in collections. Likewise, little food and flight data are available for these bats.

With the exception of *M. beccarii* and possibly *M. jugularis*, I think this group of bats may be eating small-sized, soft-bodied prey. However, if the elevated mandibular condyle is imparting an advantage in mastication and small-sized bats are relatively stronger, I believe these bats could be taking hard items as well as soft. Evidence in support of this last idea recently came to my attention when I had a chance to make a qualitative examination of stomachs of 11 *Sauromys* (specimens at the Los Angeles County Museum). The stomachs con-

tained Coleopteran remains, some moth scales, and non-moth and non-beetle remains. *Mormopterus beccarii*, because of its heavier build, could probably take more heavily armored and larger insects. Vestjens & Hall (1977) reported on the stomach contents of *Tadarida planiceps* (= *Mormopterus*) and *T. loriae* (= *Mormopterus*). In the 17 specimens of *planiceps* there were 10 occurrences of Lepidopteran remains, eight of Coleopteran remains (one each of Carabidae, Dysticidae, Scarabaeidae, and Curculionidae, and four unidentified), eight of Hymenopteran remains (seven of Formicidae and one unidentified), five of Hemipteran remains (two Pentatomidae and one unidentified), one of Insecta (Blattodea), and one of unidentified insects. This evidence seems to support my ideas presented above.

All but *M. phrudus* and possibly *Sauromys* have broad wing tips, and I suspect they are more maneuverable in flight than most other molossids, especially because of their small size. If roosting places are any evidence at all for support or nonsupport of flight activity in bats, then the following notes are necessary. *Mormopterus minutus* has been found in a "rather tall palm" (Silva-Toboada & Koopman, 1964, estimates 13 m), *Copericia vespertilionum*, in open savannah country which contained scattered clumps of scrub and palmettos (Sanborn, 1953). *Mormopterus norfolkensis* has been found roosting in buildings; *M. planiceps*, in hollow trees (McKean & Hamilton-Smith, 1967); and *M. loriae*, in roofs of houses (McKean & Price, 1967). *Sauromys* has been found in association with *T. aegyptiaca bocagei*, a small subspecies, along the Limpopo river in Southern Rhodesia (Irwin & Donnelly, 1962). This is a riparian situation, but it is a hot dry river valley of the low veld containing sandstone cliffs and acacia trees. Both bats were found under sandstone slabs on hillsides during the day. At night *Sauromys* and a large *Tadarida* were flying as high as 37 m. *Sauromys* has been found in the very dry Namib desert in southwestern Africa and has been known to live on insects and no additional water (Roer, 1971). The insects in the area (dry river beds) were Coleoptera, Lepidoptera, and Hymenoptera. Bruce Hayward (personal communication) stated that *Platymops* and *T. aegyptiaca* are often found in the same places in Kenya, namely in dry areas under flakes of rocks.

Molossops-Neoplatymops-Cynomops-Myopterus

The four remaining genera in the immediate vicinity of *Mormopterus* in the PCA plots are *Molossops*, *Neoplatymops*, *Cynomops*, and *Myopterus* (fig. 4). All are genera with one, two, or three species and together form a somewhat diffuse conglomerate on the positive side of *Mormopterus* and on the more positive end of axis II. *Molossops*, *Neoplatymops*, and *Cynomops* are New World and mostly South American; while *Myopterus* is from Africa. Bats in this group tend to have thickish dentaries and broad faces (figs. 17, 18). All have widely separated ears, no anterior sagittal crest development, no anterior palatal emargination, and no development of wrinkles on the lips. They have no development of the basi-sphenoid pits except for *Myopterus*, which has very deep ones (table 6, appendix A).

The smallest species in this conglomerate and among the smallest species in the family are two South American genera, *Molossops temminckii* and *Neoplatymops mattogrossensis* (fig. 17).

Molossops temminckii is the smallest bat in the study (GSL = 13.2 mm, table 1). It is medium in most jaw proportions (relative dentary thickness is 12 per cent,

table 6), but its mandibular condyle is elevated above the toothrow more than in any other molossid (relative height is 20.0 per cent), its ears are separated, its basisphenoid pits are nonexistent, its lips are without wrinkles, and its wing tips are broader than in any other molossid (relative length of second phalanx is 20.0 per cent).

Molossops is clustered nearest *Neoplatymops* in all three analyses but its next nearest neighbor in size-in and correlation is *Mormopterus loriae* and in size-out is *Cynomops planirostris* (table 7). The PCA distorts the relationship between these closest neighbors. The size-out distance of 0.491 between *Molossops* and *Neoplatymops* places the two among the dispersed averages in Table 5, but at a distance which separates two species much less two genera, the figure is not great and is actually less than the one separating the two species of *Myopterus*. Nearest neighboring genera (table 8) after *Neoplatymops* are *Cynomops* at 0.579, *Myopterus* at 0.618, *Promops* at 0.704, and *Mormopterus* at 0.706. The farthest genus from *Molossops* is *Otomops* at 1.262.

Neoplatymops mattogrossensis, another small bat with a GSL of 13.9 mm, is similar to *Molossops* except that its jaw proportions are even more like those in *Mormopterus* including a thinner dentary and higher coronoid process (fig. 17). *Neoplatymops* has a very elevated jaw joint (relative condylar height is 18.6 per cent) like that of *Molossops* but its wing tips are less broad (relative length of second phalanx is 12.3 per cent) than those of *Molossops* (table 5); its ears are separated, but it has shallow basisphenoid pits and its lips appear slightly wrinkled. Other individualistic features are an almost complete posterior commissure on M^3 (*Molossops* has less than one-half of the cusp present), a vestigial PM^3 (other conglomerate members have none), and the largest ears, relatively, of any other species in the conglomerate. These last features are very like those of *Mormopterus*, and the only difference apparent is that *Neoplatymops* completely lacks the palatal emargination, whereas *Mormopterus* has a well-developed one.

Neoplatymops is nearest *Molossops* in all three clustering analyses (table 7), and its next nearest species in all analyses is *Mormopterus minutus*, another very small bat (GSL = 13.4 mm).

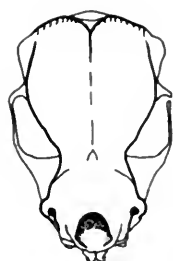
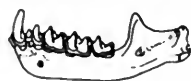
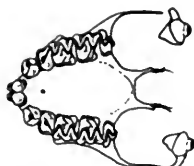
Besides *Molossops*, the next nearest taxa are *Cynomops* at 0.640, *Myopterus* at 0.668, and *Mormopterus* at 0.681 (table 8). I think this latter neighbor is not nearer as one might expect, because the first average is made from only three rather similar species of *Cynomops*, the second average from only two species of *Myopterus*, and the third is made from seven rather divergent species of *Mormopterus*.

Jaws in *Molossops* and *Neoplatymops* have the combined qualities of both *Cynomops* and *Mormopterus*, namely moderately thick jaws and well-elevated condyles above the toothrow, respectively. With the strength of the first and the possible mechanical advantage of the second, these little bats may well be able to eat both hard and soft-shelled items within their size range. *Neoplatymops* is one of the flat-headed bats (Peterson, 1965) and has a relatively high coronoid process (like that in *Sauromys*), which as mentioned in the *Mormopterus* account, may be related to a lateral shift in the location of the temporal muscle on the flattened skull. Food data for *Molossops* and *Neoplatymops* are nonexistent.

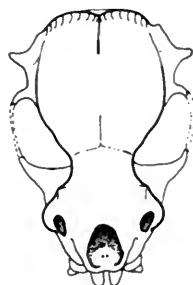
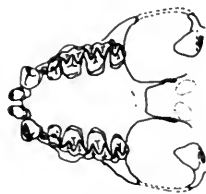
Likewise, no data exist for the speed of flight or the maneuverability of these two bats. *Molossops* has been found in decaying wood of a log (Walker, 1975) that may have been in a forest of some sort. Fenton (1972) reported that Neo-



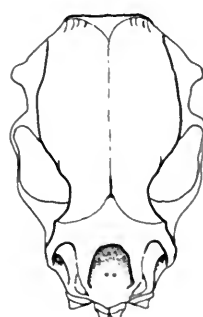
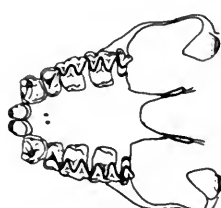
Molossops (Molossops) temminckii ♀



Molossops (Neoplatymops) mattogrossensis ♂



Molossops (Cynomops) planirostris ♂



Molossops (Cynomops) greenhalli ♂

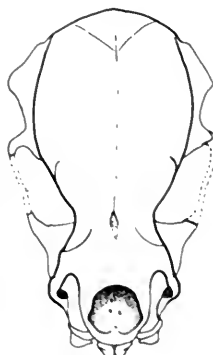
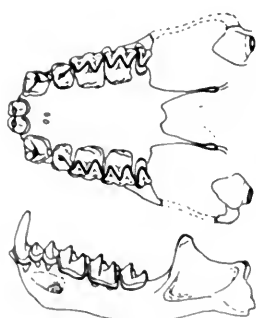


FIGURE 17.

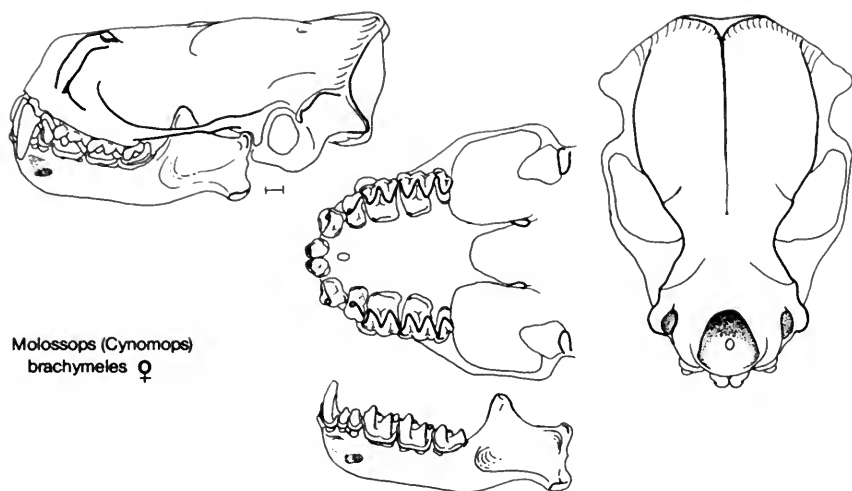


FIG. 17. Five species of *Molossops*, including *Neoplatymops* and *Cynomops*. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandibles are given for each species. The treatment of *Neoplatymops* and *Cynomops* as subgenera is explained in the Evolutionary Relationships section.

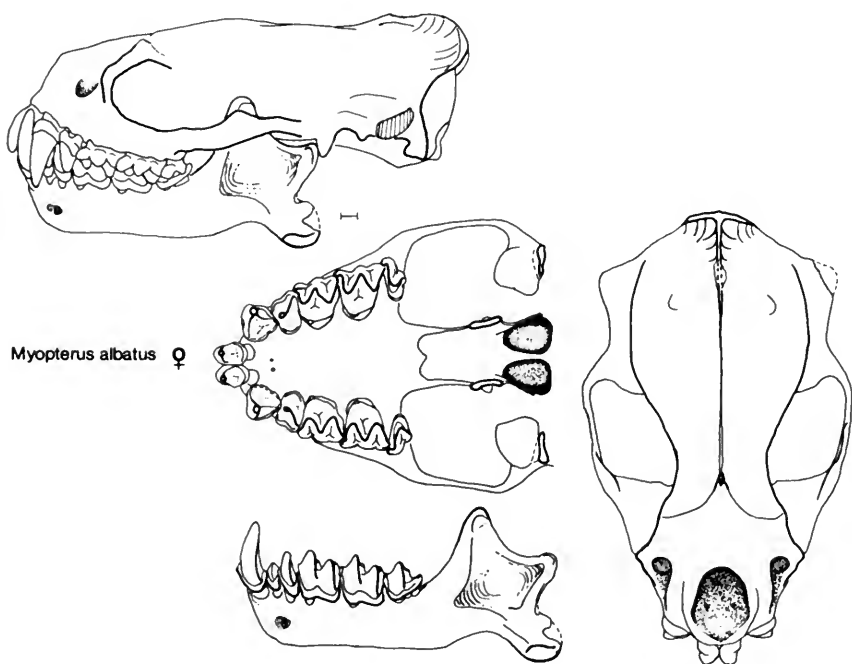


FIG. 18. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Myopterus*.

tropical species of *Molossops* along with three other molossids are caught only in the canopy. *Neoplatymops* has been found "underneath a stone out in the savannahs" of British Guiana (Peterson, 1965) and at "the edge of a small lagoon in an area made up of stone ledges, sparsely covered by a shrubby xerophytic vegetation called 'caatinga'," in eastern Brazil (Sazima & Taddei, 1976). These authors suspect that, with roosts at ground level, *Neoplatymops*, in order to take flight, "may require a flight capacity not generally seen in molossids." I doubt that *Neoplatymops* is unusual in its flying ability because I have seen *Tadarida brasiliensis*, a larger bat but one with similar wing tips (relative length of second phalanx of 12.0 per cent), take off readily from the ground.

Species of *Cynomops*, *C. brachymeles*, *C. greenhalli*, and *C. planirostris*, have slightly thicker jaws than those in *Mormopterus* (mean relative dentary thickness is 12.3 per cent), shorter coronoid processes, and a slightly less elevated mandibular condyle (mean relative height of condyle is 14.5 per cent). The three species have completely lost the PM³ and posterior commissure on M³. Combining these features with the absence of a palatal emargination and presence of sturdy beaklike incisors makes *Cynomops* much like *Molossus* and unlike the variable *Mormopterus*. Wing tips are narrow (mean relative length of second phalanx is 7.6 per cent), but this feature is obscured on axis IV. The large *Cynomops brachymeles* is a robust bat, larger than the largest *Mormopterus* and reminiscent of the larger *Myopterus*; whereas the smaller *C. greenhalli* has features closer to *Mormopterus* (for example, relative dentary thickness is only 11.3 per cent; fig. 17). The three species of *Cynomops* in the PCA plots (fig. 4) are equidistant, ignoring the immediate conglomerate members, from *Molossus*, *Mops*, and *Mormopterus* and have morphological features similar to all three.

Clustering techniques among species of *Cynomops* are no more definitive as to which group of bats are nearest to them. Size-in distances indicate that the large *C. brachymeles* is closer to the larger, thick-jawed bats of *Molossus*, *Mops*, *Promops*, and *Eumops*, whereas the two smaller-sized species of *Cynomops* are closer to the smaller *Mormopterus* and *Molossus* (table 7). The average least distance within genus (size included) is 0.570, making it third from the most dispersed taxa (table 5). Variation in size greatly affects this figure.

Size-out distances correspond well with the PCA model. Nearest neighbors of *Cynomops* in this analysis are congeners, large and small. The size-out average least distance within genus is 0.304, which is low, and makes the genus very compact, second only to *Cheiromeles* at 0.278 (table 5). Summarily, species of *Cynomops* are very similar in shape to one another.

The correlation analysis places species of *Cynomops* as most highly correlated with one another. After congeners, the neighbor most highly correlated with *C. brachymeles* is *Cheiromeles parvidens*; and the neighbor most highly correlated with *C. planirostris* is *Molossops temminckii* (table 7).

Among genera in the family, *Cynomops* is closest to genera in the conglomerate: *Molossops* at 0.579, *Neoplatymops* at 0.640, and *Myopterus* at 0.720. Closest taxa outside the conglomerate are *Mops* at 0.756 and *Mormopterus* at 0.761. The farthest neighbor from *Cynomops* is *Otomops* at 1.278 (table 8).

The species of *Cynomops* are small to medium in size: *planirostris* has a GSL of 15.4 mm; *greenhalli*, 17.4 mm; and *brachymeles*, 20.4 mm. Ecologically, I think *Cynomops* is swift flying for molossids and is endowed with medium-strong jaws. Fecal analysis of one *C. greenhalli* (table 9) showed no moth scales present, and the only cuticle remains were those of beetles. Walker (1975)

mentioned that this species in captivity took only flying termites, and that normally it roosted in hollow branches of large trees (*Tabebuia serratifolia* for one; Goodwin, 1958). *Cynomops greenhalli* has been captured over a small stream in "dense tall tropical deciduous forest" (Jones & Genoways, 1967), over a small pond just below a pine-oak zone, and over a pond and fast-running stream in dense forest (Jones & Dunnigan, 1965). LaVal (1969) reported taking *greenhalli* over a small stream bordered by low gallery forest and coffee fincas and again from tropical lowland rain forest consisting of banana groves, second growth and botanical gardens. Fenton (1972) wrote that species of *Cynomops* and *Molossops* were caught only in upper levels of the canopy. Little else is known about *Cynomops*.

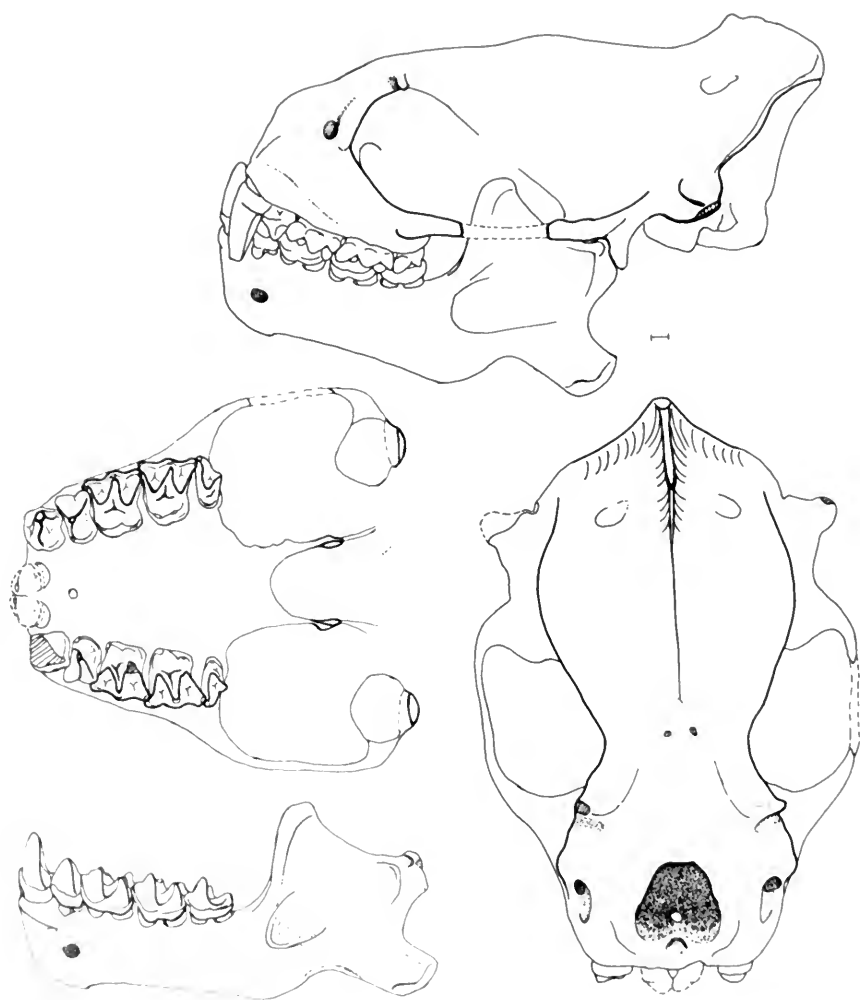
The final genus within the conglomerate group is *Myopterus*, an African genus of two species widely separated by size (fig. 19). Greatest skull length in *M. whitleyi* is 17.3 mm, whereas in *M. albatius* it is 23.5 mm (table 1). As a member of the conglomerate, *Myopterus* occupies the same general place on axis II; toward the thick-jawed, negative end (fig. 4). Though similar in condylar height above the toothrow (mean relative height is 14.0 per cent) the other jaw proportions of the two species are very divergent. The large *M. albatius* has a relatively thicker dentary (13 per cent versus 10 per cent in *M. whitleyi*), higher coronoid process (39 per cent versus 34 per cent, respectively), and greater temporal and masseter muscle moment arms (67 per cent versus 57 per cent, respectively; see table 6 for comparisons with other bats). Both *Myopterus* have broad wing tips (mean relative length of second phalanx is 17.0 per cent), and both have lost PM³ and the posterior commissure on M³. Like the other bats in the conglomerate group, these two have separated ears and unwrinkled lips; but unlike the others, the two species of *Myopterus* have deep basisphenoid pits.

The size-out distance analysis is the only one of the three clustering analyses that places the two congeners as each other's nearest neighbor. The intra-generic distance, 0.528, places *Myopterus* among the dispersed groups (table 5). Each has *Molossops temminckii* as its next nearest neighbor in this analysis.

Size-in analysis indicates that the large *Myopterus albatius* is closest to *Mops niangarae* at 0.757, and *Myopterus whitleyi* is closest to *Cynomops greenhalli* at 0.615. The size-in intra-generic distance is 1.489, the highest figure in table 5. Correlation between congeners is only 0.459. *Myopterus albatius* is most highly correlated with *Cheiromeles parvidens* at 0.476, whereas *M. whitleyi* is most highly correlated with *Molossops temminckii* at 0.555 (table 7).

Among genera, *Myopterus* is nearest *Molossops* at 0.618, *Neoplatymops* at 0.668, *Cynomops* at 0.720, and then to *Mops* (0.792) and *Mormopterus* (0.788); farthest neighbor is *Otomops* at 1.270 (table 9).

The two species of *Myopterus* are divergent not only in size but also in shape. A size-out distance of 0.528 is great for similarly shaped bats. Probably, *M. albatius* is able to consume large hard-bodied prey, while *M. whitleyi* is capable of consuming small, soft-bodied prey. No food data are available. In flight they are probably more maneuverable than most molossids and possibly slower. *Myopterus whitleyi* is known to be a species of the high forest and roosts in vegetation and sometimes houses (Rosevear, 1965). Lang & Chapin (1917), with some question, placed *M. albatius* in a group of forest species; but Hayman & Hill (1971) reported that *M. albatius* inhabits savannahs.



Cheiromeles parvidens ♂

FIG. 19. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Cheiromeles*.

Cheiromeles

At the extreme in the principal components plot in Figure 4A, *Cheiromeles* is in the most positive position. It is a genus which consists of two large species, *C. parvidens* and *C. torquatus*, and is found in Indonesia and the Philippines. These giant molossids are distinctive not only because of their size, but also because they are virtually hairless and are commonly called the naked bats or naked bull-dog bats. Species of *Cheiromeles* are the most extreme members of the Molossidae in shape as well as in size (fig. 2). They have the thickest jaws (mean relative dentary thickness is 16.0 per cent), widest face, and some of the broadest-tipped wings (mean relative length of second phalanx is 16.8 per cent) in the entire family. *Cheiromeles* is extreme in all other jaw proportions, and it has an extremely well-developed posterior sagittal crest. As a result the general appearance is one of extremely powerful jaws and strong, stocky skull (fig. 19). Like many of the other bats in this quadrate (particularly of the conglomerate) PM³ is lost as is the posterior commissure on M³, the lips are not wrinkled, the ears are widely separated, and the basisphenoid pits are nonexistent.

Cheiromeles parvidens and *C. torquatus* form the most compact pair of any two molossids in the size-in distance analysis (at 0.301) and in the correlation analysis (at 0.982). It is possible that true *torquatus* is not represented in my study, but Koopman (personal communication) questions whether these two large molossids are separate species anyway. In the size-out distance analysis the two specimens are separated by a distance of 0.278. Several other pairs of molossids with distances of less than 0.300 are suspected by me or other authors of being two members of the same species instead of two separate species.

Next nearest neighboring species to both species of *Cheiromeles*, size-in, is *Eumops underwoodi* and, size-out, *Molossops temminckii*. Next most highly correlated to *Cheiromeles parvidens* is *Cynomops brachymeles* and to *Cheiromeles torquatus* is *Eumops underwoodi* (table 7). Nearest generic neighbors to *Cheiromeles* are *Molossops* at 0.884 and *Cynomops* at 0.974, and the most distant genus is *Otomops* at 1.743 (table 8).

The specimen of *Cheiromeles torquatus* (female specimen, GSL is 29.6 mm) is slightly smaller than *C. parvidens* (male specimen, GSL is 30.6 mm), but both are closely similar in shape.⁴ I know that the great development of the posterior sagittal crest allows a large area for temporal muscle origin, and although no food data are available, the bats should be easily capable of eating large, well-armored insects. I predict that *Cheiromeles* is rather slow flying for a molossid not only because of its relatively broad-tipped wings but also because of its great weight. Harrison & Medway (1959) reported that a specimen of *Cheiromeles torquatus* in Borneo weighed about 174 gm (*Eumops perotis*, the largest North American molossid, weighs only about 53.5 gm [Vaughan, 1966]).

Medway (1958) gave an excellent account of a colony of *Cheiromeles torquatus*, some 18,000 to 20,000 individuals, roosting in Niah Great Cave in western Borneo. Though the fecal pellets were not examined closely, only exoskeletal insect fragments were found. No bird remains were found, although Medway suspected that the large bat might be feeding on the small swiftlet *Collocalia lowi* which nests in the same cave. Apparently wastes are eliminated both as feces and oral pellets. I recently examined fecal pellets taken from the floor of this cave

⁴Because *torquatus* is larger than *parvidens* (Miller & Hollister, 1921), I probably have two specimens of *parvidens*, leaving *torquatus* unrepresented here.

and found many recognizable parts of beetles and flying ants. Kitchener (1954a) reported that an individual *Cheiromeles* lived well in captivity on a diet of grasshoppers and moths.

Besides caves, *Cheiromeles* are known to live in small colonies in hollow Tapang trees (*Abauria*) (Harrison, 1954). Walker (1975) reported the large bat to have been found in rock crevices and in holes in the ground. I cannot find the source of this information, but if this heavy bat takes flight from the ground, it surely requires a tremendous amount of lift. Whether the longer phalanges of the digits and increased camber produces enough lift for *Cheiromeles* to take flight from the ground is certainly an interesting question.

An unusual adaptation in *Cheiromeles*, thought to be useful in climbing in hollow trees (Kitchener, 1954b), exists in the form of pouches under each wing which open toward the tail. These pouches are not for carrying young (usually twins) as was first thought but for the folded wing distal to the metacarpals. Only the forearm, adpressed metacarpals, and thumb protrude, enabling the bat to move agilely about.

Eumops

The final genus, and perhaps the most interesting, is the New World *Eumops*, a group almost as variable as the family itself. Seven species—*E. auripendulus*, *E. bonariensis*, *E. glaucinus*, *E. hansae*, *E. maurus*, *E. perotis*, and *E. underwoodi*—are represented in my study. They are medium to large molossids which range in GSL from 19.5 mm in *E. hansae* and *E. bonariensis* to 30.4 mm in *E. perotis* (fig. 20, table 1, appendix A).

Most variation occurs along axis II and positioning can be accounted for by the highly correlated jaw proportions, but on axes III and IV the positioning of the bats is merely an averaging of opposing and variably combined characters (fig. 4). Extremes on the jaw axis (II) are *E. perotis* with the thinnest dentary (relative thickness is 9.0 per cent) on the negative end and *E. auripendulus* with the thickest dentary (relative thickness is 14.0 per cent) on the positive end. This placement makes *perotis* much like the *Otomops*-*T. macrotis* extreme and *auripendulus* much like the *Molossus* extreme. Further, *auripendulus* has entirely lost the posterior commissure on M^3 and bears only a small PM^3 , whereas *perotis* has not entirely lost the commissure and maintains a moderate-sized PM^3 . The relatively small *hansae*, with medium dentary thickness and the most elevated jaw joint of the genus, has the most complete tooththrow with full N-shape on M^3 and moderate PM^3 . *Eumops maurus*, a slightly larger *Eumops* which is medium in all jaw proportions, has less than half the posterior commissure present on M^3 and has lost its premolar (however, specimens of *maurus* from Surinam have this tooth; Eger, 1977). The remaining three *Eumops* bear a small PM^3 , slight commissure present on M^3 , two with thin jaws (*bonariensis* and *glaucinus*), and the other, *underwoodi*, with jaws more like *auripendulus* (table 6, appendix A).

Axes III and IV are not highly correlated with the characters of the species of *Eumops*. Though several *Eumops* have large anteriorly directed ears, all except *hansae*, which has separated ears, are coded for having the intermediate condition of joining (specimens in fluid that I have recently examined show that at least *perotis* is miscoded—the ears appear to be well joined). All have moderate to deep basisphenoid pits and all have lips with the microscopic wrinkles (not deep ones). The wing tips are narrow (mean relative length of second phalanx is

6.6 per cent), and all but two have well-developed lateral lambdoidal crests (*hansae* and *bonariensis*).

In the multi-dimensional PCA plots (fig. 4), the smallest species of *Eumops*—*bonariensis* and *hansae*—are difficult to separate from *Tadarida*, *auripendulus* is difficult to separate from the *Molossus* swarm, and *maurus* and *glaucus* are close to *Promops*. *Eumops underwoodi* and *perotis*, the two largest *Eumops*, are relatively isolated from any other group.

Size-out distance indicates that six species of *Eumops* are nearest neighbors of each other (table 7). *Eumops auripendulus* is nearest *Molossus bondae*, then *M. sinaloae*, and finally *E. glaucinus*. The average least distance within the genus (size-out) is 0.560, the most dispersed average in Table 5.

Size-in distance also places six of the seven *Eumops* nearest congeners. *Eumops bonariensis* is nearest *Chaerephon nigeriae* and several other species of *Chaerephon* or *Tadarida*. The closest congeneric neighbor of *bonariensis* is *maurus*. Average least distance, size-in, for the genus is 0.607, one of the largest averages in the table (5) and one which is affected largely by size variation in the species of *Eumops*.

Clustering by correlation again indicates six of seven species to be most highly correlated with congeners. *Eumops hansae* is most highly correlated with *Tadarida aurispinosa* and next most correlated with congener, *bonariensis*. Nearest generic neighbors of *Eumops* are *Neoplaticomops* (0.782), *Chaerephon* (0.784), and *Promops* (0.818), and its farthest neighbor is *Cheiromeles* (1.404).

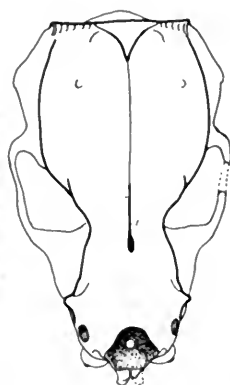
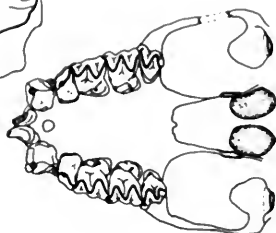
There are some interesting relationships of size and shape which occur in the jaw structure of several of the *Eumops* species. Regressions of jaw proportions on a size variable, GSL, show that *E. perotis* has uniquely thin jaws for a bat its size (fig. 7). *Eumops perotis* has well-developed jaw muscles and relatively large teeth (table 3). Besides *Cheiromeles*, *E. perotis* is one of the most extreme in molossid shapes.

With the kind of morphological variation present in the genus, food data from one species could not represent the genus as a whole. Species of *Eumops* seem to contain large and medium bats with thick dentaries and large and small bats with thin dentaries. Stomachs of six *underwoodi* (large with thick jaw) contained 47 per cent beetles, 6-10 mm in length; 31 per cent grasshoppers, 40-60 mm in length; 12 per cent leafhoppers; and 10 per cent Lepidoptera (Ross, 1967). Another stomach was found to contain four large (40 mm) June beetles (Melolonthinae) and two larger (60 mm) long-horned beetles (Cerambycidae). On the opposite extreme, *Eumops perotis* with thin jaws (sample size of nine) was found to have taken exclusively the abdomens of large hawk moths up to 60 mm long (Ross, 1967). Easterla & Whitaker (1972) reported that in 18 specimens 100 per cent contained 79.9 per cent Lepidoptera and 55.6 per cent contained 16.5 per cent Gryllidae and Tettigoniidae. Data support the prediction that a large molossid with thick jaws eats large, hard items such as beetles, and that a large molossid with thin jaws is taking and eating large soft-bodied prey such as moths.

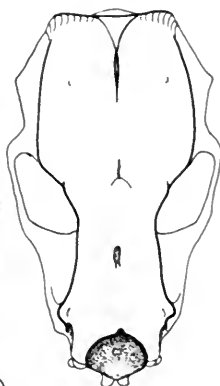
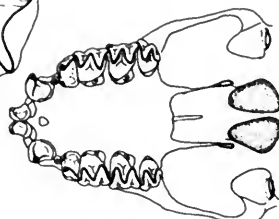
Variation in the wing tips of species of *Eumops* is not as great as in the jaw structure. All have narrow wing tips, but there are few data on the flying habits of any of the species. Vaughan (1966) has assigned *E. perotis* the highest aspect ratio in his study of several species including three molossids and has calculated that its minimum flight speed is 14.7 m.p.h., also the highest figure in the



Eumops bonariensis ♂



Eumops hansae ♂



Eumops glaucinus ♂

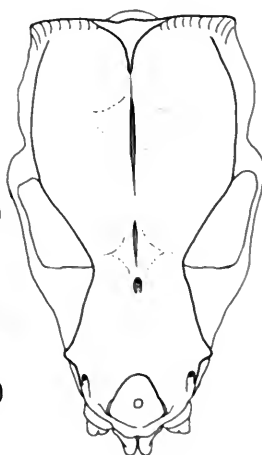
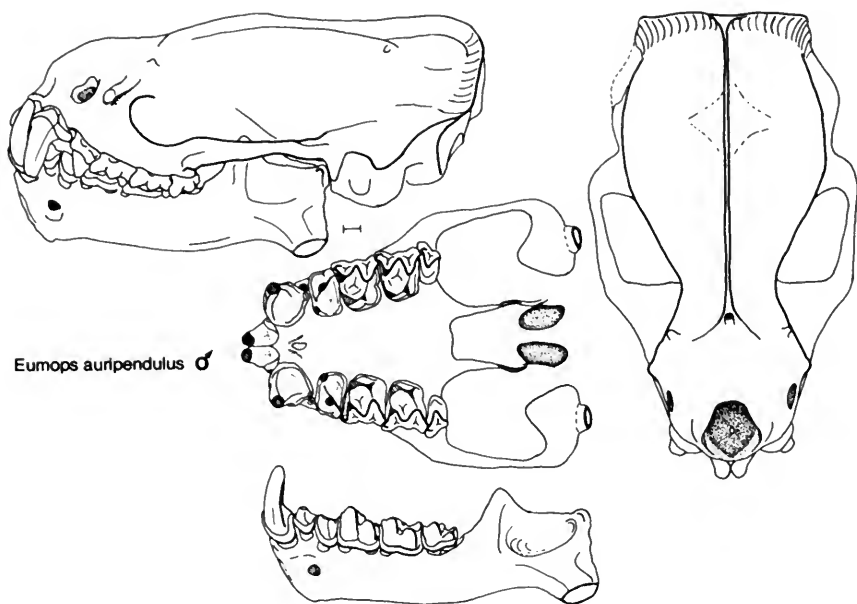
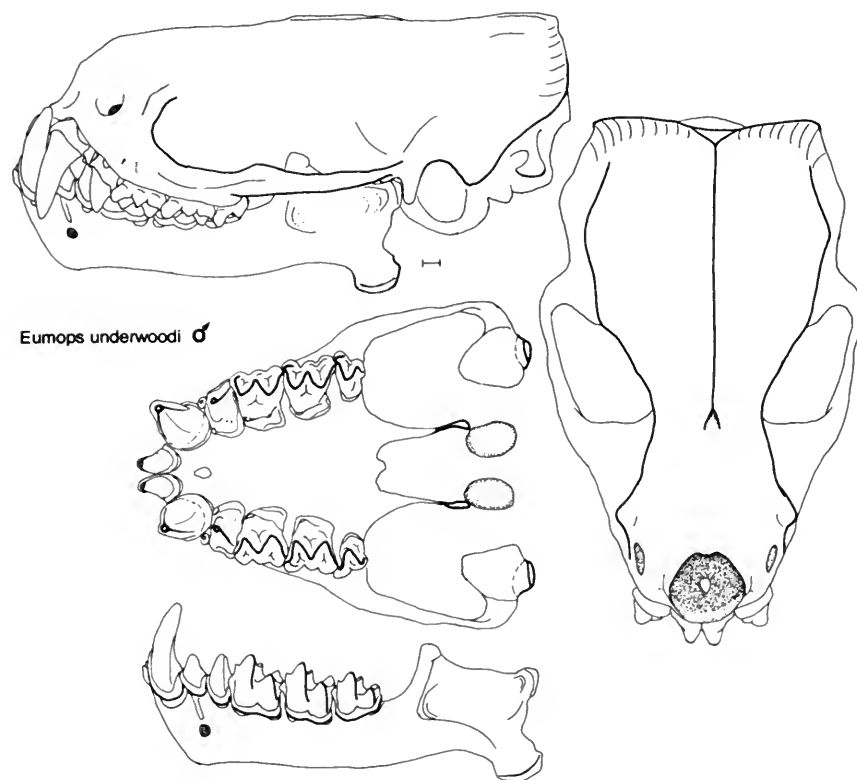


FIGURE 20.

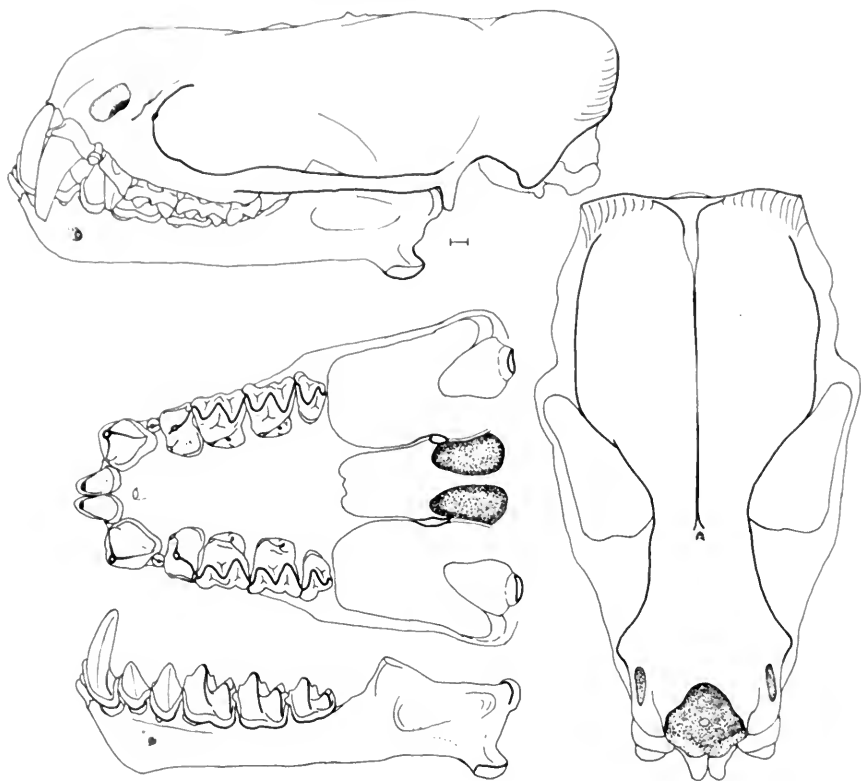


Eumops auripendulus ♂



Eumops underwoodi ♂

FIGURE 20.



Eumops perotis ♂

FIG. 20. Six species of *Eumops* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for each species.

study. These high figures make *E. perotis* the fastest flying bat in Vaughan's study. This large species of *Eumops* lives high in cliffs and is said to free-fall before it can fly. *Eumops underwoodi*, another large species, is thought to be much like *E. perotis* in that it lives in high, dry places. Findley et al. (1972) calculated the speed in *E. underwoodi* to be at least 27 m.p.h., but the authors thought this figure was an underestimate. *Eumops underwoodi* has also been found with *E. glaucinus* in tropical deciduous forest (Carter et al., 1966). LaVal (1969) reported that he took *E. glaucinus* over a shallow river surrounded by thorn forest and gallery forest. *Eumops auripendulus* has been found in belfries and roofs (Brosset & Dubost, 1967) and under loose bark (Jones, 1966), but where it flies has not been reported. Little is known about the smaller species of *Eumops* except for Fenton's (1972, p. 295) comment that *E. hansae*, as with several molossid species, is "caught only in the upper levels of the canopy." Marinkelle (1970) mentioned that a specimen of *E. bonariensis delticus* was taken in a net set in a rain forest on a river bank in southwest Colombia.

The loud noises emitted by *E. perotis* and *E. underwoodi* have been mentioned before. Whether the small species are as loud is not known. They do not all have ears as large as *E. perotis* nor do all live in dry places, leading me to suspect that their voices might be different.

Two species of vespertilionid bats, *Mimetillus* and *Nyctalus*, added to the analysis as being molossid-like have characteristics similar to *Mormopterus* but are more extreme on axis III (fig. 4, appendix A). The vespertilionids have wide faces and widely separated ears like species of *Mormopterus*, *Molossops*, *Cynomops*, and *Cheiromeles*. These two bats had to be coded in such a way as to fit into the trend of variation which occurs in molossids; hence, a coded character may not exactly describe (often an underestimate) the actual vespertilionid state and may cause these two bats to be more phenetically similar to molossids than they really are. For example, the degree of emargination of the anterior palate in the two vespertilionids is much greater than that in any species of molossid, but the two were only given the largest molossid code. Probably as a result of this underestimation, *Mimetillus* and *Nyctalus* do not appear as phenetically distinct from molossids as do the two species of *Cheiromeles* in my analysis.

ECOLOGY

What niches do molossids occupy? Is there competition for food and roost sites? How is coexistence possible? To answer these questions best, one would need to monitor the actual movements and behavior of molossids in their natural environment. Molossids, however, are difficult to capture, and because there are only a few specimens of many species, even the taxonomy of the group has not yet been adequately worked out. I think that some predictions about a molossid's ecological role can be made based on the morphology of the animal. Several authors have used this predictive method but usually with only a few morphological characters which represent trophic adaptations. Findley (1973, 1975) applied multivariate morphology to predict structure of several bat faunas. He used different distance measures and compared 1) how close, on the average, bats were to one another on different continents and in temperate or tropical regions and 2) how dispersed a fauna or community was in these places. Here, I describe the structure of three molossid bat faunas from a morphological viewpoint. At the end of the evolution section I compare the three faunas statistically and examine each for which might be the oldest fauna.

Molossids are unique among Chiroptera as the nocturnal counterparts of swifts because they are high, swift, and direct fliers (Fenton, 1975). In this habitat, probably few flying vertebrates are in intensive competition with molossids for food (although there may be more competition for shelter). Recently the subject of the ecological interaction between bats and nocturnal birds has been more fully investigated by Fenton & Fleming (1976). Chiropteran interfamilial competition for food or shelter is poorly known and outside the realm of my study. Here, I examine the family as an entity, different from other flying vertebrates, for geographical patterns in morphology and whether morphologically similar molossids are sympatric or allopatric. General ideas of intrafamilial competition among molossids are elucidated.

From the ecologically important characters that emerge from the principal components analysis, I can broadly represent the capabilities of the bats. The

authors of those papers which use few morphological traits for ecological predictions tend to use those which may show some relationship to the size, type, or consistency of prey taken, and to the size and type of shelter sought, or both. Schoener (1965, 1968) thought that sympatric congeners of birds and lizards avoid competition by concentrating on different-sized food items, whereas Tamsitt (1967), believed that the roosting site is more important in the composition of neotropical bat communities. Both McNab (1971) and Kock (1973) think that particle size of food and type or consistency of food are important parameters for successful coexistence of congeners.

Highly correlated characters from the PCA and ones I think are important in separating species of molossids in a fauna (and possibly a community) are general size (represented by GSL), which determines not only size of prey taken but also availability of roosting site; a jaw character (represented by relative dentary thickness), which determines whether hard or soft prey is taken; and a wing character (represented by relative length of the second phalanx of finger IV), which I think is related to maneuverability and speed of flight and, thus, how prey are taken or where a roost is located.

With these characters, the bats can be represented in a three-way morphological matrix, similar to the food niche matrix of McNab's (1971), where each geographic fauna is divided into cells to represent a molossid of a certain size and type (table 10). Geographic divisions correspond with the areas of concentrations of molossids: the most populated being the Ethiopian and Neotropical regions, and the least populated being the Eurasian and Australasian regions. Divisions in the size character and wing character occur at approximately 0.5 standard deviation unit from the mean and yield the categories SMALL-, MEDIUM-, and LARGE-sized bats and THIN-, MEDIUM-, and THICK-jawed bats (figs. 3, 21). I believe I can make predictions with some confidence as to habitat utilization for the small- and large-sized bats and thin- and thick-jawed bats but not for ones in the intermediate category. The wing character has a bimodal distribution, hence, the categories NARROW and BROAD wing tips. Although small, medium, and large sizes of molossids are marked off, increases of 1 mm in GSL remain in the matrix for ease of explanation. It is also possible that increments in size of this degree may be ecologically important in bats.

Taxonomically the Ethiopian and Neotropical regions have a similar composition: each has two large genera, several smaller genera, and two genera are shared. The greatest concentration of species of *Mops* and *Chaerephon* occurs in Africa. No representatives of these genera are found in the New World and only five occur in the Indo-Australian region. Similar concentrations occur in the Neotropics in species of the genera *Eumops* and *Molossus*, both of which are endemic. The smaller endemic genera are *Platymops*, *Sauromys*, and *Myopterus* in the Ethiopian region; and *Neoplatymops*, *Molossops*, *Cynomops*, and *Promops* in the Neotropics. *Otomops* is confined to both Old World areas, and *Tadarida* and *Mormopterus* are found in both the New and Old Worlds.

In general body size, medium-sized molossids compose over 50 per cent of the molossid fauna in all three geographical regions (table 10). In the two regions of highest concentration of molossid species, the Ethiopian has a greater percentage of large bats than does the Neotropical (28 per cent versus 17 per cent); while the Neotropical region has a greater percentage of small bats than does the Ethiopian (28 per cent versus 17 per cent). Bats in the Indo-Australian region follow the pattern found in the Ethiopian.

TABLE 10. Morphological niche matrix for molossid faunas based on three morphological characters: greatest skull length, jaw thickness, and wing tip width.

| GSL (mm.) | ETHIOPIAN REGION | | | | | | | | | | | |
|------------------|----------------------------------|-------------------|--|----------------------|-------------------------|----------------------------------|----------------------|------------|-------------------------|----------------------|-------------|-----------------------|
| | Medium jaw | | | | Thick jaw | | | | NEOTROPICAL REGION | | | |
| | Thin jaw Narrow wing | Broad wing | Narrow wing | Broad wing | Thin jaw Narrow wing | Broad wing | Narrow wing | Broad wing | Thin jaw Narrow wing | Broad wing | Narrow wing | Broad wing |
| 13.0 (small) | | | | | | | | | | | | |
| 14.0 | TR ACETA | | | XIPHONYC | | | | | | | | |
| 15.0 | TN NARUA PLATYRCA | | | | TR PHRID CP FIANA | | M COBEA | | TR FLANA | TR LORIA TR NOREA | | |
| 16.0 | TC CHAPI | | | TR JUCUA | T BRASIA | | | | | | | |
| 17.0 (medium) | SAURONYC MYOP MUA | | TC MAJOR TC PUMIA TC BOMBI TN LEONA | | | CP GREX PRO NASU | M MOLOSS M BONDIA | | | | | |
| 18.0 | T ANSORA TC NIGEA TC RUSSA | | | TN BRACH TN THEBA | T LATICA | | M TRINIT | | | | | TR BECTR |
| 19.0 | T AESTFA | | TC BIVIA | | T FERORA E BODADA | E HANSAA | M SINALA | | TC JONOR OTO PAPO | TC PLICA | | TN SANGA |
| 20.0 | | | | | | T AURISA E MAURUS PRO CENA | CP BBAKA M PRETIA | | | | | |
| 21.0 | TC ALOYA | | | TN NIVEI | | | M ATEBA | | OTO SECA | T KUBORI | | TC JOBEM TN MOPSA |
| 22.0 (large) | | T FULMIN T LOBATA | | | | | | | | | | |
| 23.0 | | TN TREVO | | TN NIANG PROF ALB | T MACROA | E GLAUCA | E AURIPA | | T AUSTRA | | | |
| 24.0 | | T AFRICA | | | | | | | T TENICA OTO MROA | | | |
| 25.0 | | | | TN CONGA | | | | | | | | |
| 26.0 | | | | | | | | | | | | |
| 27.0 | | | | | | | | | | | | |
| 28.0 | OTO NABA | | | TN MIDNA | | | | | | | | |
| 29.0 | | | | | | | | | | | | |
| 30.0 | | | | | E PEROTA | | | | | | | C TORQUIT C PARVID |

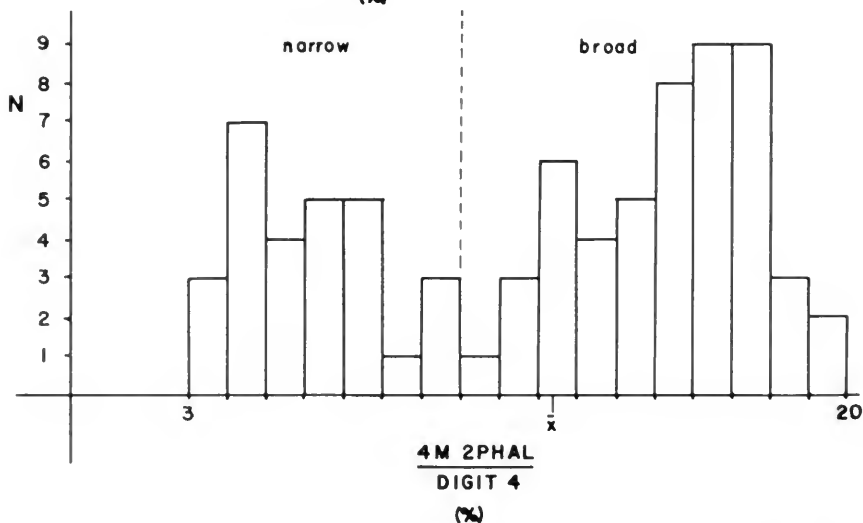
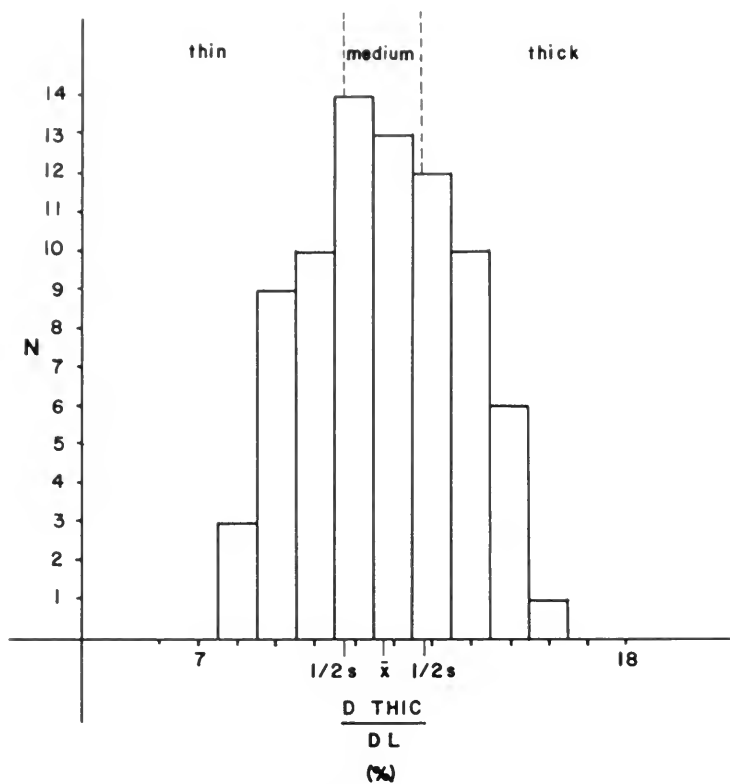


FIG. 21. Distributions of the jaw (DTHIC DL) and wing (4M 2PHAL/DIGIT 4) characters. The jaw character is divided at approximately 0.5 standard deviation units from the mean to make the categories THIN, MEDIUM, and THICK. The wing character is bimodal and divided into the categories NARROW and BROAD.

The similarity in faunas of molossids with thick and thin jaws is striking. Species of *Molossus* from the Neotropics (fig. 9) and species of *Mops* from Africa (fig. 11) represent two kinds of bats with thick jaws and well-developed sagittal crests. I think these two genera can be thought of as ecological counterparts, and both are probably consuming hard-shelled prey. A similar example can be drawn for bats with thin jaws: *Otomops martiensseni* in Africa (fig. 13) and *Tadarida macrotis* (fig. 15) in southwestern United States are both probably eating soft-shelled prey. Though both New and Old Worlds have a similar percentage of bats with thick jaws, the Old World has more bats with thin jaws. It would be interesting to know if there is a greater number of soft-bodied prey available to molossids in the Old World. Further interesting questions can be asked of the bats with thick jaws. In both the Neotropics and Africa a graduated size series of thick-jawed species occurs: Do these bats specialize on hard prey as neatly graduated in size as themselves? How big a difference in general size has to occur to allow coexistence with other similarly built molossids? On the whole, the Ethiopian fauna contains a greater variety of molossids because not only does this fauna have very small bats of both jaw extremes but also very large bats of both jaw extremes. The Neotropical fauna does not have a very large bat with thick jaws, nor does the Indo-Australian fauna have a very large bat with thin jaws.

The wing character (fig. 21) has a bimodal frequency distribution. Most of the bats with narrow wing tips are in the New World, whereas most of the bats with broad tips occur in the Old World. Two of the large African *Tadarida* (*T. africana* and *T. fulminans*) have wing tips similar (though not quite as narrow) to those of New World bats, especially species of *Eumops*. There is evidence that these two *Tadarida* roost in cliffs as do several species of *Eumops*. Similarity in the skulls of *T. africana* and *E. glaucinus*, bats of similar size, are shown in Figures 14 and 20. Possibly the two *Tadarida* are ecological vicars with some of the species of *Eumops*. Randolph Peterson (personal communication) suggested that *T. lobata*, another similar, large African species, is especially *Eumops*-like because of its long, narrow rostrum. One last pair of ecological (if not phylogenetic) counterparts exist with species of *Myotis* in Africa and *Cynomops* in the Neotropics (figs. 18, 17).

Only five New World species possess broad wing tips, and all are small species: *T. brasiliensis*, two species of *Mormopterus*, and two monotypic genera, *Molossops* and *Neoplatymops*. Most of the 17 small molossid species in the world have broad wing tips. In the New World, however, there are exceptions: a species of *Molossus*, a species of *Cynomops*, and a species of *Mormopterus*, all three of which have narrow wing tips.

The remaining New World *Tadarida* (the *T. macrotis* group), *Eumops*, *Molossus*, and *Promops*, possess extremely narrow wing tips. What is it about the New World environment that selects for narrow-tipped wings in molossids? Are ancestors of these bats ones which may have migrated from the Old World? Although the last is an intriguing question, the bats that today appear to be most closely related to Old World forms, *Tadarida brasiliensis* and one or two species of *Mormopterus*, are bats with relatively broad wing tips. Also, the long-distance yearly migrations which occur in the New World are undertaken by both *T. brasiliensis* and *T. macrotis*.

Simplified faunal pictures such as the matrix in Table 10 are interesting, but are they helpful when realistically looking at a community of sympatric species?

Though the known geographical ranges of molossids are far from accurate, I think even the most general prediction of possible intrafamilial competition adds to the knowledge that now exists for molossid species.

Overlap in the morphological cells in the matrix means that the bats involved are approximately the same size, fly in a similar way, and feed on the same types of insect prey. In cells of overlap it would be helpful to know whether the molossids are allopatric, sympatric, or syntopic. Allopatry is not very interesting to the present coexistence of species, although it may represent a result of earlier competition or isolation. It is the sympatric situations that require close examination. Field data to clarify whether the sympatric species are actually syntopic are not always at hand. In any case it may be instructive to see if the overlapping species are also nearest phenetic neighbors in the 76-character space described in the first section.

Two overlapping, small Ethiopian molossids with broad wings and thin jaws, *Mops nanula* and *Platymops*, are mostly allopatric. The first is a western forest species (Rosevear, 1965); whereas the second, an eastern species, lives in narrow crevices in dry, open areas (Hayward, personal communication). There may be some geographical overlap in western Kenya where *M. nanula* has been found in light, riverine forest in dry, grassy *Acacia* country (Start, 1969). *Platymops* is one of the flat-headed molossids and lives in very narrow crevices.

The medium-sized *Sauromys petrophilus* and *Myopterus whitleyi* are also separated geographically and ecologically. *Sauromys*, another flat-headed molossid, is a southern African dry country species (Irwin & Donnelly, 1962); whereas *Myopterus whitleyi* is a western and central forest species.

Three overlapping medium-sized species with broad wings and thin jaws are *Tadarida ansorgei*, *Chaerephon nigeriae*, and *C. russata*. These three are near neighbors morphologically (see table 7), and are all found in Zaire. That they are actually syntopic is not known. *Tadarida ansorgei* is a savannah species and prefers to roost in rocks (Allen et al., 1917; Verschuren, 1957), whereas *Chaerephon nigeriae* is a species of the Guinea woodland, also savannah country, but roosts in trees or houses (= *cistura* of Allen et al., 1917; Koopman, 1965). Fenton & Peterson (1972) reported *russata* to be consistently associated with the edge of "invasive Guinea woodland" near "high forest" (terms after Rosevear, 1965). Seemingly these three species have slightly different niches, even if they were to be syntopic.

Another cell having overlap occurs with four species of medium-sized bats with broad wings and medium-thick jaws: *Chaerephon bembelini*, *C. major*, *C. pumila*, and *Mops leonis*. The species of *Chaerephon* are near neighbors of one another (table 7) but not of the species of *Mops*. *Mops leonis* is a high forest species which roosts in trees and under roofs (Rosevear, 1965). Though all three species of *Chaerephon* are inhabitants of Zaire, they have not been found at the same locality. *Chaerephon bembelini* is thought to be associated with mixed forest rather than dense high forest or open savannahs (Peterson, 1971b), whereas *C. major* is more of an inhabitant of the savannah (Verschuren, 1957; Hayman & Hill, 1971). Both species are known to roost in rocks. *Chaerephon pumila* has been reported from dense gallery forest (Verschuren, 1957) and from open woodland (Rosevear, 1965). It is a common and widespread bat which roosts in tree holes and houses. These four, if syntopic, would be interesting to study to see how their coexistence is possible.

Two medium-sized, broad-winged bats with thick jaws, *Mops brachyptera* and *M. thersites*, are thought to be either allopatric, closely related forms or subspecies of one another (Koopman, 1975). *Mops thersites* is the western form and found in the high-forest zone (Rosevear, 1965); but *M. brachyptera*, the eastern form, is very poorly known.

Mops demonstrator and *Mops condylura* are not only the same size with similarly shaped wings and jaws, but they are also syntopic. Both have been found in the Garamba National Park in Zaire, both roost in the tree, *Vitex doniana*, and both live in apparently the same savannah habitat (Verschuren, 1957). However, the two are never found together in the same roost but maintain monospecific groups. *Mops condylura* is one of the most common molossids and one that also inhabits man-made habitations. Verschuren noted that although the two animals when alive are very similar to one another, *M. demonstrator* (Faradjius in his report) is not as clumsy or heavy in appearance as *M. condylura*. The two are nearest phenetic neighbors.

The last overlap consists of *Mops niangarae* and *Myotis albatrus*, both large bats with broad wings and thick jaws. Both were found near Niangara in northeastern Zaire by Lang & Chapin (1917), and both were listed as being found in rain forest or extensive gallery forest (Allen et al., 1917). Hayman & Hill (1971), however, reported that *Myotis albatrus*, in contrast to *Myotis whitleyi*, "seems to be an inhabitant of the savannahs." Lang & Chapin had remarked, too, that they thought *Mops niangarae* should also be found in more open country. Where these two large species actually live and how they coexist is simply not known. Although *niangarae* is the nearest neighbor to *albatrus*, the size-in distance is great (0.757, table 7), and the two are not nearest neighbors in the size-out analysis. The two are not alike phenetically and probably have different ecological requirements.

A more obvious question may be asked while looking at the morphological niche matrix: Do molossids that we know are sympatric overlap on the matrix? Two early studies which involve all the Chiroptera in an area have been most useful for examination of sympatric species of molossids. Allen et al. (1917) listed which bats were collected at each of their localities (area of 30- to 40-mile radius from the locality) in northeastern Zaire. I think molossids collected at one place can be thought of as sympatric species, though not necessarily as syntopic ones.

At Faradje, *Tadarida ansorgei*, *Chaerephon chapini*, *C. major*, *Mops demonstrator*, *M. trevori*, and *M. midas* were captured. None of these overlap in the matrix (table 10). At Medje, *C. russata*, *M. leonis*, *M. condylura*, and *M. congica* were found; and none of these overlap in the matrix. At Niangara, *C. nigeriae* (originally called *cistura*, see Koopman, 1965), *M. nanula*, *M. niangarae*, and *Myotis* overlap but probably are not syntopic. In general, the matrix is a fairly good ecological separator of molossids, as each of these sympatric bats has a cell (and by inference, ecological niche) to itself.

Verschuren (1957) studied the ecology of bats in Garamba National Park, an area of 480,000 hectares, in northeastern Zaire. I also consider molossids found here sympatric: *T. ansorgei*, *C. pumila* (including *limbata*), *C. major*, *M. condylura*, *M. demonstrator*, *M. midas*, *M. trevori*, and *Otomops martiensseni*. Hayman & Hill (1971) reported the later collection of *C. nigeriae* from this park. Several overlaps occur, but these can be explained. *Tadarida ansorgei* and

Chaerephon nigeriae are not found in the same locality in the park, and though both occur in the savannah habitat, they prefer different roosts. *Chaerephon pumila* and *C. major* are also found at different localities in the park, but even so, *pumila* seems to prefer the forest and *major*, the savannah. Though similar in habits and habitat as mentioned earlier, *Mops condylura* and *M. demonstrator* never occur together in the same roost. *Mops condylura* also makes use of houses for roosting but *M. demonstrator* does not. These two are probably closely related sibling species and are coexisting as a result of man's activities.

Verschuren reported several occurrences of groups composed of two species. One contained 150 *M. condylura* and one *M. trevori*, another contained equal small numbers of *C. major* and *T. ansorgei*, and a third small group contained *M. demonstrator* as the dominant and *M. midas* as the subordinate. Neither member of these pairs overlap on the matrix. One is either larger or of different wing or jaw shape than the other or has a combination of differences in the three characteristics.

Four overlaps occur in the Indo-Australian matrix, but the species of each overlapping pair seem to be allopatric (table 10). Few specimens and fewer field data are available for the species in this region. There is doubt as to whether some of the taxa are really specifically distinct. The three small species of *Mormopterus* are probably confused taxonomically (McKean & Price, 1967), and there is some doubt as to whether *Cheiromeles* contains two species or one (Koopman, personal communication). Until more specimens and data are available, little more can be said about this situation.

Neotropical molossids also overlap in several places on the morphological niche matrix. Unfortunately, fewer field data are available concerning the actual ecology of these bats. A study such as that of Verschuren (1957) has not been completed. Three small bats with medium-thick jaws and broad wing tips are *Mormopterus minutus*, *Molossops temminckii*, and *Neoplatymops mattogrossensis* and overlap on the matrix. *Mormopterus minutus* from Cuba is allopatric with the other two species which are probably sympatric in eastern South America. *Molossops* has been found in a decaying log, possibly indicating a mesic place, and *Neoplatymops* has been found in a xeric place under a slab of rock in a savannah (Peterson, 1965). The latter is the only New World flat-headed molossid.

Data on the remaining overlaps in Table 10 for New World molossids are spotty and are listed with few or no comments. Two pairs appear to be allopatric: *Mormopterus phrudus* from Peru and *Cynomops planirostris* from central and eastern South America; and *Tadarida femorosacca* from western and central Mexico and southwestern United States and *Eumops bonariensis* from southern Mexico and south into South America. Two other pairs seem to be allopatric for most of their distribution but may be sympatric in a small portion of it. *Cynomops brachymeles* from much of South America and *Molossus pretiosus* from Mexico, Central America, and Colombia have both been found in Venezuela. *Cynomops greenhalli* from Mexico, Central America, and Colombia and *Promops nasutus* from Paraguay, Brasil, and Venezuela have both been found on Trinidad. Only two pairs remain which are sympatric through most of their distribution. *Molossus bondae* and *Molossus molossus* are found in most of Central America, Colombia, and Venezuela. No data exist suggesting factors which may allow coexistence of these two very similar bats. *Tadarida aurispinosa* and *Promops centralis* are allopatric with *Eumops maurus*, but the two are sympatric with each other in

western Mexico and probably in South America. Whether the two are syntopic is unknown.

McNab (1971) reported that tropical molossid faunas on a number of smaller islands in the Caribbean are made up of similar kinds of bats. He noted that in several cases at least a small species of *Molossus* and a small species of *Tadarida* are found together and that "there must be some important ecological segregation of those bats such as the level or area at which feeding occurs." From the matrix and from food data presented in the first section, I expect that because of the different dentary configurations, the species of *Tadarida* may well be concentrating on small, soft prey and the species of *Molossus*, on small, hard prey.

I suggest in the preceding discussion that there are few instances of morphologically overlapping sympatric molossids in the Neotropics and none in the Indo-Australian region compared to the Ethiopian fauna. Perhaps this means that molossids in the Neotropical and Indo-Australian faunas presently suffer less from intrafamilial competition than molossids in the Ethiopian fauna.

EVOLUTIONARY RELATIONSHIPS

Are molossids which are phenetically similar also closely related phylogenetically, or are they similar because they share an overall convergence of characters? Few data exist on ancestors of molossids, data which might have aided this discussion. Smith (1976) recently reviewed the known fossil Chiroptera, and Slaughter (1970) summarized the evolutionary trends of chiropteran dentitions. Because evidence from fossils is scanty, I feel justified in using the multivariate shape analyses coupled with several evolutionary theories to determine phylogenetic relationships among species in the family Molossidae. In this section, I discuss the overall phenetic groupings of molossids as summarized by the phenogram of the size-out distance matrix and decide what species form what I think are the natural genera based on similarity of shape. Additionally, I point out several characters that can be graded as to their primitive and derived nature in order to evaluate the phylogenetic relationships in the family. Although this is primarily a phenetic study, I present some idea as to which are the primitive and derived genera in the family. A final question is how have molossids radiated through time, and what is the geographic distribution of primitive and derived forms of molossids.

Two clustering methods concerned with shape relationships are the size-out distance analysis and the correlation analysis (table 7). Not only does the size-out distance analysis appear less affected by general size difference among the bats than does correlation, but also the phenogram from the size-out matrix has a higher co-phenetic correlation coefficient than does the correlation phenogram (0.754 versus 0.678). This coefficient indicates how well the phenogram represents the matrix from which it is taken; and though one is higher than the other, both indicate a level of representation of their respective matrices used by other authors (Schnell, 1970; Findley, 1972). The size-out analysis and phenogram are the basis for the following discussion, but evidence from the correlation analysis is included to enhance understanding of the shape relationships. A summary of each bat's nearest neighbor or most highly correlated neighbor is presented in Table 7.

Across the size-out phenogram in Figure 22, I have drawn two solid lines at

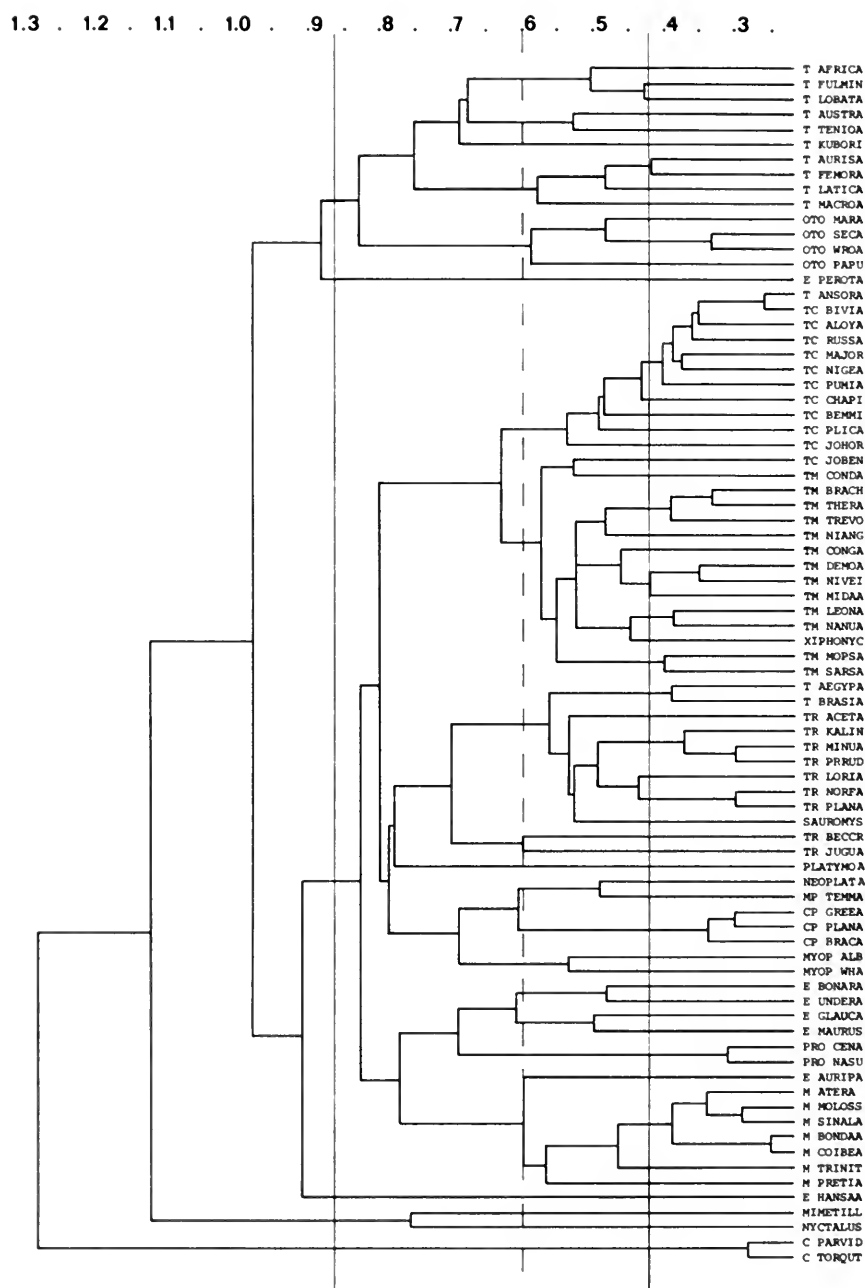


FIG. 22. Phenogram of molossidids taken from the size-out distance matrix. Solid lines at 0.420 and 0.870 are the means of least and average distances, respectively, of the matrix. The dashed line at 0.600 is the line used to delineate 12 molossid genera of similar dispersion.

0.420 and at 0.870. The first is the average nearest-neighbor-distance computed from the distance matrix from which the phenogram was taken, and the second is the average value of all the elements of that matrix. Several genera are more tightly packed than others and the two lines are good indicators of the relative dispersion in each molossid genus. A third of the junctures occur at the level of the first line and 90 per cent, at the level of the second. The dashed line at 0.600 is the line I use to delineate 12 molossid genera of similar morphological dispersion. Seventy-five per cent of the junctures occur by the level of this line. The phenogram is most accurate at representing the data at the smaller distances where the bats are most alike and few averages have been taken, but is not as good at representing the greater, intergroup distances, where averages of averages occur.

In addition to the basic phenetic arrangement of the species, I use several ideas about evolution to help me interpret the relationships among the species. The first concerns the use of primitive and derived characters. Only a few of the 76 characters are conducive to this use because most of the quantitative characters cannot be classed as primitive or derived either because of size or functional morphology. The characters remaining are the multistate codes which I feel have some phyletic use when compared to the Vespertilionidae, a family of bats thought to be more primitive than molossids (table 11). No basisphenoid pits, widely separated ears (usually short and erect or perky), no wrinkles on the lips, a deeply emarginated anterior palate, a long second phalanx of digit IV, and 32 teeth are primitive states for molossids. The primitive tooth formula is $\frac{1.1.3.3}{1.1.3.3} = 32$ where the I_3 and the PM^3 are well-developed, M^1 with distinct metaconule, and M^3 with a complete N-shaped cusp pattern (premetacrista present). Deep basisphenoid pits, well-joined ears over the nose (usually large and slouched or bonneted), finely wrinkled lips, no anterior emargination of the palate, short phalanx on digit IV, and 26 teeth are derived conditions. The derived formula is $\frac{1.1.1.3}{1.1.1.3} = 26$ with PM_3 vestigial, M^1 without metaconule, and M^3 with premetacrista absent.

Because of the small sample size for each species and the subjectivity of the coded characters, I cannot discuss each slight change in each code for each species. The dental characteristics, because they are easier to determine (although toothwear is occasionally a problem), are given slightly more attention, especially if corroborated by other traits. In the section on generic considerations that follows, I summarize the specific relationships by examining the phyletic relationships (both phenetically and cladistically) among the genera.

The second and third ideas about evolution more or less help me define what a genus is within the Molossidae. My thoughts coincide with those of Maglio (1973, p. 14) who said, "All members of a genus share a fundamental adaptive zone different in some particular way from that of other such groups. This adaptive zone may or may not be precisely definable, but is inferred by the common possession of a particular suite of functionally integrated characters." More specifically, a genus tends to be made up of several animals of different sizes but with one basic shape, and the very large species are often allometrically much distorted compared to that basic shape. Probably evolutionarily, the easiest change to make is in size, not in shape. Schoener (1965, 1968) mentioned that, ecologically, species are more likely to expand first on a food axis of items of different size rather than a habitat axis. I assume the first axis has to do with size and the second with shape. Simpson (1944, p. 92) gave

TABLE 11. Primitive-derived traits for all molossid species, arranged in the same order as those in the phenogram (fig. 22); character states of seven of the traits are in Materials and Methods section. Within each column, the primitive state is on the left and the derived on the right, and the position of each number in the column visually reflects this. Broad (B) and narrow (N) wing tips are determined in the Ecology section (fig. 21), and actual number of lower incisors is given.

| | EAR 123 | PITS 12345 | PALATE 54321 | WRINKLES 1234 | WING BN | INCISORS 642 | PM ³ 4321 | M ¹ 321 | M ³ 123456 |
|----------|----------------|----------------|-----------------|------------------|------------|-----------------|-------------------------|-----------------------|--------------------------|
| T AUSTRA | 2 | 1 ^a | 4 | 3 | B | 4 | 2 | 3 | 1 |
| T TENIOA | 2 | 3 | 4 | 2 | B | 6 | 4 | 3 | 1 |
| T AFRICA | 2 | 4 | 4 | 4 | N | 4 | 2 | 2 | 3 |
| T FULMIN | 2 | 3 | 4 | 4 | N | 4 | 4 | 2 | 3 |
| T LOBATA | 2 | 3 | 4 | 4 | N | 4 | 4 | 1 | 3 |
| T KUBORI | 2 | 1 ^a | 4 | 3 | B | 4 | 4 | 2 | 1 |
| T AURISA | 3 | 3 | 3 | 2 | N | 4 | 4 | 3 | 1 |
| T FEMORA | 2 | 2 | 3 | 2 | N | 4 | 4 | 3 | 1 |
| T LATICA | 3 | 2 | 3 | 3 | N | 4 | 3 | 3 | 1 |
| T MACROA | 3 | 4 | 3 | 2 | N | 4 | 4 | 3 | 1 |
| OTO MARA | 3 | 5 | 3 | 4 | B | 4 | 4 | 1 | 1 |
| OTO SECA | 3 | 5 | 3 | 4 | B | 4 | 4 | 1 | 1 |
| OTO WROA | 3 | 5 | 3 | 4 | B | 4 | 4 | 1 | 1 |
| OTO PAPU | 3 | 5 | 3 | 4 | B | 4 | 4 | 1 | 1 |
| E PEROTA | 2 ^b | 4 | 1 | 4 | N | 4 | 3 | 2 | 4 |
| T ANSORA | 3 | 3 | 3 | 2 | B | 4 | 3 | 2 | 3 |
| TC BIVIA | 3 | 3 | 3 | 3 | B | 4 | 3 | 2 | 3 |
| TC ALOYA | 3 | 4 | 2 | 3 | B | 4 | 3 | 3 | 3 |
| TC MAJOR | 2 | 2 | 2 | 2 | B | 4 | 3 | 2 | 3 |
| TC NIGEA | 3 | 3 | 2 | 3 | B | 4 | 3 | 2 | 3 |
| TC PUMIA | 3 | 3 | 2 | 3 | B | 4 | 2 | 2 | 3 |
| TC CHAPI | 3 | 3 | 2 | 2 | B | 4 | 3 | 2 | 3 |
| TC RUSSA | 3 | 3 | 2 | 3 | B | 4 | 3 | 2 | 3 |
| TC BEMMI | 3 | 2 | 3 | 2 | B | 4 | 4 | 2 | 2 |
| TC PLICA | 3 | 3 | 2 | 3 | B | 4 | 4 | 2 | 2 |
| TC JOHOR | 3 | 3 | 2 | 3 | B | 4 | 3 | 1 | 2 |
| TC JOBEN | 3 | 3 | 2 | 2 | B | 4 | 3 | 1 | 2 |
| TM CONDA | 3 | 2 | 2 | 3 | B | 4 | 2 | 2 | 4 |
| TM BRACH | 3 | 3 | 4 | 2 | B | 4 | 3 | 2 | 4 |
| TM THERA | 3 | 3 | 3 | 2 | B | 4 | 3 | 2 | 4 |
| TM TREVO | 3 | 4 | 2 | 3 | B | 4 | 3 | 1 | 4 |
| TM NIANG | 1 | 4 | 2 | 3 | B | 4 | 3 | 1 | 4 |
| TM CONGA | 3 | 4 | 2 | 3 | B | 4 | 2 | 2 | 5 |
| TM DEMOA | 3 | 4 | 2 | 2 | B | 4 | 2 | 2 | 5 |
| TM NIVEA | 3 | 3 | 2 | 2 | B | 4 | 2 | 1 | 5 |
| TM MIDAA | 3 | 3 | 2 | 2 | B | 4 | 2 | 2 | 5 |
| TM LEONA | 3 | 2 | 3 | 2 | B | 4 | 3 | 2 | 5 |
| TM NANUA | 3 | 2 | 3 | 2 | B | 4 | 3 | 2 | 5 |
| XIPHONYC | 3 | 2 | 3 | 2 | B | 2 ^c | 4 | 1 | 5 |
| TM MOPSA | 3 | 3 | 3 | 2 | B | 4 | 1 | 2 | 6 |
| TM SARSA | 3 | 3 | 2 | 3 | B | 4 | 1 | 2 | 6 |
| T AEGYPA | 1 | 3 | 4 | 2 | B | 4 | 3 | 3 | 2 |
| T BRASIA | 1 | 2 | 4 | 2 | B | 6 ^c | 2 | 3 | 1 |

TABLE 11. *Continued.*

| | EAR 123 | PITS 12345 | PALATE 54321 | WRINKLES 1234 | WING BN | INCISORS 642 | PM ³ 4321 | M ¹ 321 | M ³ 123456 |
|----------|------------|---------------|-----------------|------------------|------------|-----------------|-------------------------|-----------------------|--------------------------|
| TR ACETA | 1 | 2 | 4 | 3 | B | 6 | 1 | 2 | 1 |
| TR KALIN | 1 | 1 | 4 | 1 | B | 4 | 1 | 3 | 1 |
| TR MINUA | 1 | 2 | 3 | 1 | B | 4 | 1 | 2 | 1 |
| TR PHRUD | 1 | 2 | 3 | 1 | N | 4 | 1 | 3 | 1 |
| TR LORIA | 1 | 2 | 4 | 1 | B | 4 | 2 | 1 | 2 |
| TR NORFA | 1 | 2 | 4 | 1 | B | 4 | 2 | 3 | 1 |
| TR PLANA | 1 | 2 | 4 | 2 | B | 4 | 3 | 3 | 2 |
| SAUROMYS | 2 | 2 | 4 | 1 | B | 4 | 2 | 3 | 2 |
| TR BECCR | 1 | 2 | 4 | 2 | B | 4 | 1 | 3 | 1 |
| TR JUGUA | 1 | 2 | 4 | 1 | B | 6 | 2 | 3 | 1 |
| PLATYMOA | 1 | 1 | 3 | 3 ^d | B | 4 | 1 | 3 | 2 |
| NEOPLATA | 1 | 2 | 1 | 2 | B | 4 | 2 | 1 | 2 |
| MP TEMMA | 1 | 1 | 1 | 1 | B | 2 | 1 | 1 | 4 |
| CP GREEA | 1 | 1 | 1 | 1 | N | 4 ^c | 1 | 1 | 5 |
| CP PLANA | 1 | 1 | 1 | 1 | N | 4 | 1 | 1 | 5 |
| CP BRACA | 1 | 1 | 1 | 1 | N | 4 | 1 | 1 | 5 |
| MYOP ALB | 1 | 5 | 1 | 1 | B | 2 | 1 | 1 | 5 |
| MYOP WHA | 1 | 4 | 1 | 1 | B | 2 | 1 | 1 | 5 |
| E BONARA | 2 | 4 | 1 | 4 | N | 4 | 2 | 2 | 3 |
| E UNDERA | 2 | 3 | 1 | 4 | N | 4 | 2 | 1 | 4 |
| E GLAUCA | 2 | 4 | 1 | 4 | N | 4 | 2 | 2 | 4 |
| E MAURUS | 2 | 3 | 1 | 4 | N | 4 | 1 ^c | 2 | 4 |
| PRO CENA | 2 | 3 | 1 | 1 | N | 4 | 2 | 1 | 5 |
| PRO NASU | 2 | 3 | 1 | 1 | N | 4 | 2 | 1 | 5 |
| E AURIPA | 2 | 4 | 1 | 4 | N | 4 | 2 | 1 | 5 |
| M ATERA | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M MOLOSS | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M SINALA | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M BONDAA | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M COIBEA | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M TRINIT | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| M PRETIA | 2 | 3 | 1 | 1 | N | 2 | 1 | 1 | 6 |
| E HANSAA | 1 | 5 | 1 | 4 | N | 4 | 2 | 3 | 1 |
| MIMETILL | 1 | 1 | 5 | 1 | N | 4 | 1 | 3 | 1 |
| NYCTALUS | 1 | 3 | 5 | 1 | N | 4 | 3 | 1 | 1 |
| C PARVID | 1 | 1 | 1 | 1 | B | 2 | 1 | 1 | 5 |
| C TORQUT | 1 | 1 | 1 | 1 | B | 2 | 1 | 1 | 5 |

^aLong, shallow grooves instead of pits.^bMiscoded; ears are definitely joined with a band over the nose.^cVariable number of lower incisors.^dDifficult to code because upper lip is covered with thick hairs or spines.

an example from fossil-browsing horses which expand on a size basis before shifting into a grazing mode of existence.

Third, the notion of Cope's Rule, as elucidated by Stanley (1973), is that it may be easier for animals to radiate from a small than from a large relative body size, and that very large animals mark the end of some line of radiation. Thus, in each group discussed, I examine the large and small members of the group as well as which of the animals have primitive or derived characteristics.

Specific Considerations

The uppermost part of the phenogram is occupied by *Tadarida* from the Old and New Worlds, *Otomops*, and *Eumops perotis* (fig. 22). Bats of this assemblage are all located on the far negative end of axis II of the PCA (fig. 4), meaning they have thin jaws and probably eat moths and other insects with soft bodies. To show the similarities in the general form of four of the largest bats, drawings of their skulls are shown in Figures 13-15 and 20.

The first six OTU's (fig. 22) are species of *Tadarida* from the Old World and bats of more or less large size (GSL = 21.0 to 24.0 mm). All have some kind of basisphenoid depression (although *australis* and *kuboriensis* were not coded as such because their "pits" are atypically long with indistinct margins, fig. 14), joined ears, wrinkled lips, and emarginated anterior palate. *Tadarida teniotis*, with its well-developed I₃, has the most primitive tooth configuration of any molossid. All six bats have a PM³ but whether it is large or small varies. Most have a metaconule present on M¹ and all have the premetacrista on M³, but both teeth vary in their development (table 11). The large African *Tadarida africana*, *T. fulminans*, and *T. lobata* join together at 0.500, after *fulminans* and *lobata* form a pair first at 0.430. The close similarity of these three bats has been noted by several authors. Peterson & Harrison (1970) and Peterson (1974) compared and contrasted *lobata* with the other two, and Harrison (1971) compared *africana* with *lobata* and *fulminans*. These three may be slightly more derived than the other three because of their narrower wing tips, more finely wrinkled lips, and less development of the metaconule on M¹ and premetacrista on M³.

At 0.520, *T. teniotis* and *T. australis* join together. Hill (1961) thought *T. australis* was more similar to *T. aegyptiaca* in spite of its greater size, but he also mentioned that it should be thought of as "an isolated and outlying member of that subgenus [*Tadarida*]." McKean & Calaby (1968) concluded that *australis* is closely related to *T. kuboriensis*, another Australasian molossid, but that its skull is longer than that of *kuboriensis*. Both shape-clustering analyses place *australis* closest to *teniotis*. Because of this and because *teniotis* is a widespread species, I think *australis* and possibly *kuboriensis* are Australasian relatives of *teniotis*. *Tadarida teniotis* is found between latitudes 20° and 40° N in the Palearctic region and is the only molossid to live this far north all year.

The three large African *Tadarida* join the *teniotis-australis* pair at 0.670. Koopman (1975) placed the large *africana*, *fulminans*, *lobata*, and *teniotis* in his *T. teniotis* group of large forms. Thomas (1891) mentioned that some relationship with the large African forms and *teniotis* exists, particularly with respect to *lobata*. This last affinity was reviewed by Peterson & Harrison (1970) and Peterson (1974). The three seem equally derived over *teniotis* because they retain only four lower incisors and a less than completely shaped N on the M³. The PM³ is well developed in all three, though possibly less so in *africana*, the largest species of *Tadarida*. These six molossids are nearest neighbors of one another

and are most highly correlated with one another, but two other bats are phenetically related to them, namely *Tadarida brasiliensis* and *Tadarida aegyptiaca*. Aellen (1970) noted that the shape of the baculum in *T. teniotis* resembles that in *T. brasiliensis*.

Koopman (1975, p. 424), after clearly demarcating species in the subgenus *Chaerephon*, restricted "typical *Tadarida* to the *teniotis* group, *aegyptiaca* and *brasiliensis*." These last two bats have a definite similarity with *Tadarida*: *T. aegyptiaca* is most highly correlated with *teniotis*, and *brasiliensis* is highly correlated with *aegyptiaca*. The two are also each other's nearest neighbor, size-out, but their next nearest neighbors are species of *Mormopterus*; hence, their placement on the phenogram. I discuss these two bats later, but phenetically they are similar to both *Tadarida* and *Mormopterus*.

Tadarida kuboriensis joins the five *Tadarida* at 0.690. This bat is nearest *brasiliensis* (0.578) size-out, but most highly correlated with *australis*. *Tadarida kuboriensis* averages nearer *Tadarida* than to any other genus on the phenogram. Actually *australis* and *kuboriensis* are similar, and in an analysis where only raw data are used (no codes or ratios) *kuboriensis* is closest to *australis* in all three clustering methods. McKean & Calaby (1968) have also pointed out the similarity between these two species, and Koopman (1975) included *kuboriensis* in *australis*. Why a rather great size-out distance exists between the two Australasian *Tadarida* (0.602) is difficult to explain.

New World *Tadarida* (without *T. brasiliensis*) form a distinct cluster of four species: *aurispinosa*, *femorosacca*, *laticaudata*, and *macrotis*. The first juncture occurs at 0.420, connecting *aurispinosa* and *femorosacca*, a pair which had a history of taxonomic confusion, until Carter & Davis (1961) resolved the situation. *Tadarida laticaudata* joins the two at 0.480, and *T. macrotis* joins the three at 0.570. The four form what Miller (1902) called the genus *Nyctinomops* (*Tadarida* at the time was called *Nyctinomus*) and what Shamel (1931) named the *T. macrotis* group of New World *Tadarida*. Because these four species form a distinct group in this analysis, I recommend that Miller's name, *Nyctinomops*, be resurrected. This group is distinct from the *T. brasiliensis* group of Shamel because of its short second phalanx of digit IV and its narrower rostrum, characters also included in this analysis. The derived traits of the *macrotis* group over *brasiliensis* are the loss of I₃, the shortening of the second phalanx of digit IV, the well-joined ears, and the slightly narrower palatal emargination (table 11). Exactly how these four species I now call *Nyctinomops* are phylogenetically related with the remaining species of *Tadarida* is unclear. Although a phenetic connection with them via *T. brasiliensis* is logical because of the latter's close geographic occurrence with the *macrotis* group, there is only slight support from the size-out analysis and little more from correlation. The *macrotis* group (*Nyctinomops*), however, averages closer to the Old World *Tadarida* than to any other genus (table 8). Specific neighbors which are almost as close are members of *Chaerephon* (including *ansorgei*) and *T. teniotis*. Because of the similarity of the anterior palatal emargination with certain species here included in *Chaerephon*, Koopman (1975) did not include these *Tadarida* from the New World (or *T. australis* and *T. kuboriensis*) with his "typical *Tadarida*." The difference in the configuration of the wing tips of the *macrotis* group (*Nyctinomops*) and that of *Chaerephon* is considerable, even greater than the difference between that of the former and of *T. brasiliensis* (table 6).

The largest species of *Nyctinomops* is *macrotis* (GSL = 23.3 mm), and it ap-

pears to be the largest in a graduated size series starting with *laticaudata* (GSL = 18.0 mm) shown in Figure 15. Because of this graduated series, I think a close phylogenetic relationship of *macrotis* with a molossid of another group is unlikely. The fact that *macrotis* is most highly correlated with *Otomops martiensseni* is, I believe, due to convergence. *Otomops martiensseni* is also the largest member of a graduated series of species of *Otomops* (the smaller specimens were not available for drawing; fig. 13). There are also several differences between the two genera in the primitive-derived traits. Species of *Otomops* have extremely deep basisphenoid pits, finely wrinkled lips, no metaconule on M¹, and broad wing tips (table 11).

Otomops here consists of four species of medium to large size (GSL = 19.5 to 27.0 mm). *Otomops secundus* from New Guinea joins *O. wroughtoni* from India at 0.330. The large African *O. martiensseni* joins the *secundus-wroughtoni* pair at 0.480, and the small Papuan *O. papuensis* joins the other three at 0.580. Closest neighbors of each species both in size-out and correlation are congeners. Simpson (1945) placed *Otomops* in the genus *Tadarida* (*sensu lato*). When codes and ratios are omitted from the analysis, some of the species of *Otomops* do have nearest neighbors among species of *Tadarida* and *Nyctinomops*, especially *T. teniotis*. Whether the similarity with *teniotis* is one of close phylogenetic affinity or convergence, as with *N. macrotis*, is unknown. Because *teniotis* is a large species of *Tadarida*, I suspect that the phylogenetic relationship is more likely to be with a smaller ancestor of *teniotis*. The phenetic relationship with *teniotis* is not a strong one.

Last is the juncture of *Eumops perotis* with *Tadarida* and *Tadarida*-like bats at 0.920. Though the nearest or most highly correlated neighbors of *E. perotis* are congeners, species of *Tadarida*, *Nyctinomops*, and *Otomops* average closer. Distance from nearest neighbor, *E. bonariensis*, is 0.702, the greatest distance from any nearest neighbor, but the neighbor most highly correlated is *E. underwoodi* at 0.795, a substantially high correlation. *Eumops perotis* is probably ecologically convergent with the *Tadarida*-*Nyctinomops*-*Otomops* group to which it is attached. *Eumops perotis*, like *N. macrotis* and *O. martiensseni*, is the largest in a graduated series of congeneric species that look very much alike (fig. 20). All three of these large bats have long, thin jaws, and large, slouched ears joined by a band over the nose and wrinkled, expandable lips. *Eumops perotis* and *N. macrotis* both have narrow wing tips, whereas *O. martiensseni* has broad ones. All three tend to live in arid regions and may migrate to or inhabit more temperate regions (*E. p. trumbulli* is more mesic), and I suspect all three eat soft-bodied creatures like moths. *Eumops perotis*, *N. macrotis*, and *O. martiensseni* seem to have converged toward a mutual and successful skull and body design which meets the needs of their similar life styles and feeding habits. *Eumops perotis* does have the additional derived characters of lacking the palatal emargination and having less-developed PM³ and M³ (table 11).

In the next assemblage, all of the species of *Chaerephon* are joined together at 0.540 (fig. 22). This low numerical juncture means that the bats of this group are less dispersed morphologically than typical *Tadarida*, that is, they look more like one another. Species of *Chaerephon* are medium in size and have thin jaws like those of *Tadarida* but are different from *Tadarida* in other jaw characteristics. All have four lower incisors, but the posterior commissures on M³ and PM³ in most species of *Chaerephon* are slightly less developed than those teeth in *Tadarida*, and the metaconule on M¹ is less distinct. *Chaerephon* is a slightly more derived

genus of molossids than *Tadarida*, not only because of dental traits but also because the palatal emargination is only a small notch in most of the species, and most have well-joined ears (table 11).

Features in addition to palatal emargination, and M^3 and PM^3 development which are classical characters used to distinguish *Chaerephon*, were used to determine the species positions on the phenogram (fig. 22). The majority of bats in this cluster group in much the same fashion even when the classical characters, described by codes, are removed from the analysis. Nearest neighbors both in size-out and correlation analyses are species of *Chaerephon*.

At the top of the cluster (fig. 22) *ansorgei* and *bivittata* join at 0.260. Recently, both Randolph Peterson and Judy Eger (personal communication) mentioned that they think these two are synonymous, and the low distance at which the two bats join in my study supports their idea. The two are each other's closest neighbor in both size-out correlation analyses. Koopman (1975) mentioned that *ansorgei* and *bivittata*, along with *bemmelini*, are similar, but he placed them in *Tadarida* where they must go if *Chaerephon* is conventionally defined by the shape of the palatal emargination. Differences among these three bats are discussed in the first section, but they may be slightly more primitive species of *Chaerephon* (table 11). Hayman & Hill (1971) placed *ansorgei* in *Tadarida* and *bivittata* and *bemmelini* in *Chaerephon*. I recommend that all three are species of *Chaerephon*.

Chaerephon aloysiisabaudiae joins the *ansorgei*-*bivittata* pair at 0.350, followed by *russata* at 0.360. Peterson (1969) thought *aloyisabaudiae* to be the closest relative of *russata*. Additional comparisons and similarities between these two and with *bivittata* were pointed out by Peterson (1967, 1971b) and by Fenton & Peterson (1972). Both *aloyisabaudiae* and *russata* are nearest *ansorgei* in size-out distance, but although *russata* is most highly correlated with *ansorgei*, *aloyisabaudiae* is most highly correlated with *russata*.

Chaerephon major and *C. nigeriae* form a pair at 0.370 before joining the cluster containing *ansorgei*, *bivittata*, *aloyisabaudiae*, and *russata* at 0.390. As for opinions concerning relationships of these two bats by previous authors, Rosevear (1965) noted that the skull of *major* is the same general form as that of *pumila* but is larger, whereas that of *nigeriae* is broader and flatter than that of *major*. Both *major* and *nigeriae* are nearest *bivittata* in size-out distance. In correlation, *major* is most highly correlated with *chapini* and *nigeriae*, with *russata*.

Chaerephon pumila joins the cluster at 0.400, followed by *chapini* at 0.430. Kock (1969) thought *chapini* and *pumila* should be regarded as conspecific, and although Koopman (1975) disagreed with that conclusion, he thought that the two are closely related. This analysis places both as nearest neighbors (size-out) of *bivittata*. *Chapini* is most highly correlated with *major* and *pumila* is most highly correlated with *chapini*.

Chaerephon bemmelini joins the cluster of species of *Chaerephon* at 0.480. Peterson (1971b) believed that the closest relative of *bemmelini* is *bivittata*. This study agrees with that conclusion in both shape analyses. This bat, like *bivittata*, has been frequently allied with species of *Tadarida* (Thomas, 1903; Koopman, 1975).

The last two forms to join bats in this cluster are two Indo-Australian species, *plicata* and *johorensis*, at 0.490 and 0.540, respectively. Hill (1961) reported *johorensis* to be externally much like *plicata* (except for a complex ear juncture); its skull differs from that of *plicata* by having a more flattened rostrum. He

compared only Indo-Australian members of *Chaerephon*. *Chaerephon johorensis* is nearest in distance to *chapini* and most highly correlated with *bemmelini*, whereas *plicata* is nearest *bivittata* and most highly correlated with *pumila*.

Miller (1907) claimed that *Chaerephon* closely resembles *Tadarida* (including *Nyctinomops*) except in the shape of the palatal emargination (the first are shallow, the second deep). Species of *Chaerephon* and *Tadarida* have had a long history of being included in or excluded from a single taxon. In my study each is a distinct cluster, but the two do have many characteristics in common. The fact that *ansorgei*, *bivittata*, and *bemmelini* have been difficult to place indicates to me that they are probably phylogenetically related to both *Tadarida* and *Chaerephon*. The last bat, *bemmelini*, along with the Indo-Australian species, has a slightly more primitive dental pattern than do most of the species of *Chaerephon* (table 11).

One of the largest species of *Chaerephon*, *aloyysiabaudiae*, has an elongate, narrow rostrum and a distinct metaconule on M^1 , features more typical of *Tadarida*. If large size does mark the end of a shape line, then *aloyysiabaudiae* may be paralleling the *Tadarida*-like shape. It could be that *Chaerephon* is the small-sized counterpart of *Tadarida* and that to become a larger *Chaerephon* is really to become *Tadarida*-like.

The other large bat classically placed in *Chaerephon* is *jobensis*. This bat, although its tooth configuration is characteristic of species of *Chaerephon*, has features of the jaw and skull which are similar to those of *Mops*. I think *jobensis* has taken advantage of a way of life different from that of typical species of *Chaerephon* because it is located in a geographical area where there are no species of *Mops*.

Species of *Mops* form an assemblage about as dispersed as species of *Chaerephon* and consist of bats which have medium to thick jaws, robust skulls, and body sizes that vary from small to large (fig. 22). These bats are positive on axis II and axis IV but negative on axis III (fig. 4). Because of their jaw structure, I suspect that species of *Mops* eat hard-bodied insects, like beetles, but actual data are scanty. Primitive and derived configurations of the teeth are not clear. Most species have four lower incisors (one has only two), but variation in PM^3 ranges from well developed to vestigial and even absent in two species. Diminution of PM^3 does not always occur with the diminution of the posterior commissure on M^3 . All species have at least a small notch which is a remnant of the palatal emargination, shallow to deep basisphenoid pits, and wrinkles on the lips. All but one (*niangarae*) have joined ears (table 11).

At 0.520, two bats, *C. jobensis* and *M. condylura*, join the main cluster of species of *Mops*. *Chaerephon jobensis*, as one might expect, has the more primitive tooth configuration: PM^3 is moderately developed and M^3 is well developed as in *C. johorensis*. Although *jobensis* is a large species of *Chaerephon*, it is like *Mops* because of its well-developed sagittal and lambdoidal crests and thick jaws (fig. 12). The bat with which *jobensis* joins, *M. condylura*, has been suggested by Rosevear (1965) to be intermediate between *Chaerephon* and *Mops* because *condylura* has a smaller anterior emargination and slightly better developed M^3 than most species of *Mops*. There are species of both *Mops* and *Chaerephon* that have only a notch remaining of the palatal emargination, so that this character is not a good one to use in determining which is more primitive or derived. *Mops condylura* has distinctly thick jaws and a well-

developed sagittal crest, characters shared with other species of *Mops*. The last upper molar retains a slight posterior commissure (less than half the length of the second ridge), and PM³ is vestigial. Both are traits more derived than those of species of *Chaerephon*, but may be less derived than those of other species of *Mops*.

If *jobensis* and *condylura* are intermediate between *Chaerephon* and *Mops*, what is the nature of their relationship with the two groups? *Chaerephon jobensis* is considered by Hill (1961) to be a closely related but distinct Australasian representative of *C. plicata*. He wrote (p. 54), "The skull differs little from that of *T. plicata* in structural details but is rather more heavily built. The anterior upper premolar is sandwiched tightly between the canine and PM⁴; the anterior lower premolar is only slightly reduced." *Chaerephon jobensis* is closest to species of *Mops* both in size-out and correlation, but because of its large size and *Chaerephon*-like teeth, I suspect it is derived from earlier, smaller bats of the genus *Chaerephon* and has more recently taken to eating harder-shelled prey.

Mops condylura, on the other hand, is closest to *M. demonstrator* in size-out and correlation analyses but also is of medium size and has *Mops*-like teeth. Koopman (1975), also noticed the similarity between *condylura* and *demonstrator* and thought the two are closely related. *Mops condylura* appears to be a widespread and adaptable bat with several related forms. It may well have a close relationship with *Chaerephon* as Rosevear (1965) suggested, but here *condylura* is assigned to *Mops*. Koopman (1975) and Hayman & Hill (1971) concurred with this assignment.

The main cluster of species of *Mops*, like those of *Chaerephon*, are bats connected by small distances. These thick-jawed bats have no nearest neighbors, by any of the three clustering methods, outside their group and maintain a distinct, compact cluster. Like the case with the cluster of species of *Chaerephon*, even when raw data alone are used, a similar compact cluster of species of *Mops* results.

Recently, Koopman (1975) placed five molossids in the *Tadarida* subgenus, *Xiphonycteris*, because they share the reduced M³ and well-developed anterior emargination. My analysis does not separate these molossids from other species of *Mops* which have a reduced M³ but small palatal emargination. Two of these five, *brachyptera* and *thersites*, pair at 0.330. Each is the other's nearest or most highly correlated neighbor. The pair is joined by *trevori* at 0.390 and by *niangarae* at 0.470, two included in the *midas* group of large forms of *Tadarida* (*Mops*) of Koopman (1975). These four bats have all been coded for having moderately developed PM³ and M³ with less than one-half development of the posterior ridge present. Although *trevori* is nearest *thersites*, size-out, and most highly correlated with *niangarae*, *niangarae* is both nearest to and most highly correlated with *trevori*. Whether *niangarae* is a distinct species or synonymous with *trevori* has been a matter of conflict among previous authors (Koopman, 1965; Hayman & Hill, 1971; Peterson, 1972; Koopman, 1975). Peterson discussed fully the relationship between *trevori* and *niangarae*, synonymized the latter with the first, and subsequently compared *trevori* with *congica*, another similar large bat. Koopman (1975) agreed "reluctantly" to this arrangement, but until more specimens can be collected, I am inclined to keep *niangarae* as a distinct taxon because of its more robust jaw, separated ears, and only average distance to nearest neighbor *trevori* (0.417). Peterson (1972) thinks the condition of the ears

in the type and only known specimen was distorted in preparation and that the difference in robustness is due to sexual dimorphism, both of which are quite possible.

In the next subgrouping of species of *Mops*, *demonstrator* and *niveiventer* pair at 0.350, joined by *midas* at 0.420 and *congica* at 0.460. The first two are each other's closest neighbor in both shape analyses. *Mops midas* and *congica* are both nearest *demonstrator* in distance, but are each other's most highly correlated neighbors in correlation. All four of these bats have been coded for having a small PM³ (vestigial in *demonstrator* and *niveiventer*) and for the complete lack of a posterior ridge on M³. This dental configuration could be construed as being slightly more derived than that of the *brachyptera-niagarae* subgroup. Also, *midas* and *congica* are the largest species of *Mops*. Koopman (1975) put *demonstrator* and *niveiventer* into his *T. (M.) mops* group of small forms, and *congica* and *midas* into his *T. (M.) midas* group of large forms. Koopman thought that *demonstrator* is most closely related to *niveiventer*, but emphasized that the latter has often been confused with *condylura*. He suggested the probability of intergradation between *niveiventer* and *demonstrator*. Hayman & Hill (1971) mentioned that *congica* looks like a large specimen of *condylura*, a resemblance which only remotely unites the large and small species in this subgroup. Although at one time *trevori* was included as a subspecies of *congica* by Koopman (1965; the first being a savannah species and the second a forest-living one), Peterson (1972) separated the two as distinct species. The connection of the first subgroup containing *trevori* and *niagarae* and the second containing *congica* and *midas* occurs at 0.520.

Three small species make the next subgroup: *Mops leonis* pairs with *M. nanula* at 0.390, followed by *Xiphonycteris spurrelli* at 0.450. These three have shallow basisphenoid pits and retain PM³ but have lost the posterior commissure on M³. *Xiphonycteris spurrelli* is distinctive because it has a large PM³ and only two lower incisors. (Randolph Peterson told me that he has recently seen specimens of *spurrelli* with two, four, and six lower incisors.) In distance, *nanula* and *spurrelli* are nearest *leonis*, and *leonis* is nearest *nanula*. In correlation, *nanula* and *spurrelli* are most highly correlated with *leonis*, but *leonis* is most highly correlated with *spurrelli*. Koopman (1975) noted the similarity between *spurrelli* and *nanula* and placed *nanula*, *leonis*, *brachyptera*, *thersites*, and *spurrelli* into *Tadarida* (*Xiphonycteris*). Others have noticed the resemblance among these bats. Rosevear (1965) mentioned the similarity between *leonis* and *thersites*, the skull of the former being "slighter in general appearance" than that of the latter. Hayman & Hill (1971) stated that the helmet-like appearance of the skull of *Xiphonycteris spurrelli* occurs in several species of *Mops*, and the authors intimate a resemblance between *spurrelli* and *nanula*, a small species of *Mops*. Koopman thinks these two small bats may be conspecific. I see no reason to keep *Xiphonycteris* as a valid name, even as a subgenus; the name *Mops spurrelli* is sufficient. This subgroup of three joins the first two subgroups at 0.520.

The final two species of *Mops* are Indo-Australian. *Mops mops* and *M. sarasinorum* pair at 0.400 and join the main body of the species of *Mops* at 0.550, a juncture slightly less than that of *C. jobensis* and *M. condylura*. *Mops mops* and *M. sarasinorum* are not only each other's nearest and most highly correlated neighbors, but both have a slightly more derived toothrow than that in the African species: neither has a PM³ and their M³ is highly reduced (table 11).

Their next nearest neighbors are species of African *Mops* rather than species of Indo-Australian *Chaerephon*, including *C. jobensis* (table 7).

Chaerephon and *Mops* join at 0.630 units, a distance less than that joining the Old and New World *Tadarida* (0.750). Originally designated as independent genera, *Chaerephon* and *Mops* have more recently been thought of as subgenera of *Tadarida* (Simpson, 1945; Ellerman & Morrison-Scott, 1951), but these two do form distinctive clusters in my multivariate study. The trend in diminution of PM^3 and the posterior ridge on M^3 are losses in the toothrow which occur in the New World genera as well.

Mormopterus and *Mormopterus*-like bats follow the cluster of species of *Mops* in the phenogram (fig. 22). In general, *Mormopterus* is a genus in which bats are small, have a well-developed M^3 , tall posteriorly curving coronoid process, medium-thick jaws, separated ears, shallow basisphenoid pits, and unwrinkled lips. These bats may take soft and hard prey of small size, though few data are available. On the three axes of the PCA, they are located in the center of axis II, toward the positive end of axis III, and are slightly positive on axis IV (fig. 4).

Species of *Mormopterus* are distinct from other molossids because of the maintenance of the large, invariable, N-shaped M^3 ; while both PM^3 and I_3 are variable in their presence in the toothrow. Often in other molossids, PM^3 and posterior cusp of M^3 co-vary in absence or presence. I consider all species of *Mormopterus* to be primitive molossids, but no living species have all the primitive dental characteristics. The two African-Malagasy *Mormopterus* have six lower incisors but no PM^3 , whereas the three small Australasian species have only four lower incisors but maintain a small PM^3 . *Mormopterus doriae*, from Sumatra and not available for my study, is said to bear six incisors but no PM^3 as in the African forms (Hill, 1961). *Sauromys* from Africa has four lower incisors and a small PM^3 like the three small Australasian *Mormopterus* and *Mormopterus beccarii*, the largest species of *Mormopterus* (Australasian). I consider the New World forms of *Mormopterus* (*kalinowskii*, *phrudus*, and *minutus*) to have the most derived tooth formula because they have lost both I_3 and PM^3 . *Platymops* from Africa, another bat more distantly related to this cluster, has also lost I_3 and PM^3 (although the latter is sometimes present as a spicule which Peterson [1965] thinks is a milktooth). If *Platymops* is considered a species of *Mormopterus*, it would be the most derived Old World member.

Because of the variation in tooth configuration in species of *Mormopterus*, one might wonder about which teeth are lost through time for members of this genus. Often, teeth are eliminated by a shortening of the jaw or an enlargement of other teeth or both at once. The last upper molar is not diminished in this particular genus of small bats; only teeth in the anterior part of the jaw are the ones lost. Apparently the posterior cusp on M^3 at the posterior part of the jaw, a part where much force occurs during chewing, is more useful than those anteriorly. The complete M^3 , combined with the unusually elevated condyle above the toothrow, may give a great advantage to these small bats in cutting up their prey.

Prior to the 0.420 line, the three New World species (*kalinowskii*, *minutus*, and *phrudus*) join together, and just past this line, the three Australasian species (*loriae*, *norfolkensis*, and *planiceps*) form a cluster (fig. 22). These last three may be confused taxonomically (Johnson, 1959; McKean & Price, 1967). At 0.480, these six small-sized bats (GSL = 13.0–15.5 mm) join together to form the core of

the *Mormopterus* cluster. The relationship between these two similarly shaped but geographically distant subgroups of *Mormopterus* is, I suspect, one of recent common ancestry rather than an overall convergence of 76 characters toward a small-sized similarly shaped molossid.

Sauromys joins these six species of *Mormopterus* at 0.520 and appears more similar in shape to these bats than to any other flat-headed bat such as *Platymops*, with which *Sauromys* was considered to be congeneric at one time (Harrison, 1962). *Sauromys* is closest to *Mormopterus norfolkensis* in all three clustering analyses and shares several of the traits listed in Table 11 with Australasian *Mormopterus*. The condition of the ears of *Sauromys* is more derived than that in *Mormopterus* because they are not widely separated; the ears only just join at the bases to form a V-shaped valley. I consider *Sauromys* a subgenus of *Mormopterus* that has adapted to living under desert conditions and in narrow roosts. Peterson (1965) suggested that *Sauromys* is closest to *Tadarida* (including *Nyctinomops*) and *Mormopterus* than to any other molossid genus and is quite distinct from *Platymops*. Prior to Peterson's report, Harrison (1962, p. 763) had written that *Sauromys* was "an evolutionary connecting form" between *Tadarida aegyptiaca bocagei* (which he called primitive) and *Platymops* (which he called specialized for narrow crevices). Although my analysis cannot support or refute this idea, it does cluster *Sauromys*, *Platymops*, and *T. aegyptiaca* in the same general area of the phenogram; hence, the bats have some phenetic similarity.

At 0.530 *M. acetabulosus* from Madagascar and eastern Africa joins the main cluster of species of *Mormopterus*, bats to which it is more similar in shape than to the other species of *Mormopterus* from Madagascar, *M. jugularis*. Nearest neighbors of *acetabulosus* are New World *Mormopterus*.

Two species of *Tadarida* join the cluster of species of *Mormopterus* at 0.560. These two bats, *T. aegyptiaca* from the Old World and *T. brasiliensis* from the New World, form a pair before the 0.420 line. This low phenetic juncture between these two bats provides an interesting, unexpected similarity between molossids of the Old and New Worlds. Presently, both bats are widespread in their respective hemispheres: *T. aegyptiaca* inhabits most of Africa and southwestern Asia, while *T. brasiliensis* is found from about 40° N latitude in North America through Central America to about 40° S in South America. Similarity in shape could be due to convergence because of similar life styles; both are able to tolerate arid conditions (Harrison, 1962; Krutzsch, 1955; Hayward, personal communication) and are able to seek shelter under flakes of rocks and in narrow crevices. Their jaw proportions are similar and neither has a very narrow or very broad wing tip. *Tadarida brasiliensis* may be the more primitive molossid because it maintains six lower incisors (Slaughter, 1970), although the third lower incisor is small and often variable in its appearance (Glass, 1953), and it has only shallow basisphenoid pits. Both maintain PM³ and N-shaped M³ and both have separated ears and wrinkled lips (table 11). Although the separated ears is the only really different trait from the other species of *Tadarida*, the ears are not widely separated or short and erect as in species of *Mormopterus*, but larger and more forward-facing as in other *Tadarida*.

It is an intriguing occurrence that *T. brasiliensis* is represented by my analysis as being more similar to an African bat rather than to other New World species (*Nyctinomops* or *Mormopterus*). A close phylogenetic relationship between the two, *brasiliensis* and *aegyptiaca*, cannot be ruled out. A recent Old World-New

World exchange in the genus *Tadarida* (*sensu lato*) has heretofore been considered improbable relative to some vespertilionid Old-New World relationships (Koopman, 1970). However, my analysis, where I have tried to remove size differences among the bats, would support a more recent phylogenetic relationship between species of *Tadarida* in the Old and New World. Indeed, the resemblance between a small subspecies of *T. aegyptiaca*, *T. a. bocagei*, and *T. brasiliensis* is strong and supports the suspicion of a close phylogenetic relationship (fig. 23).

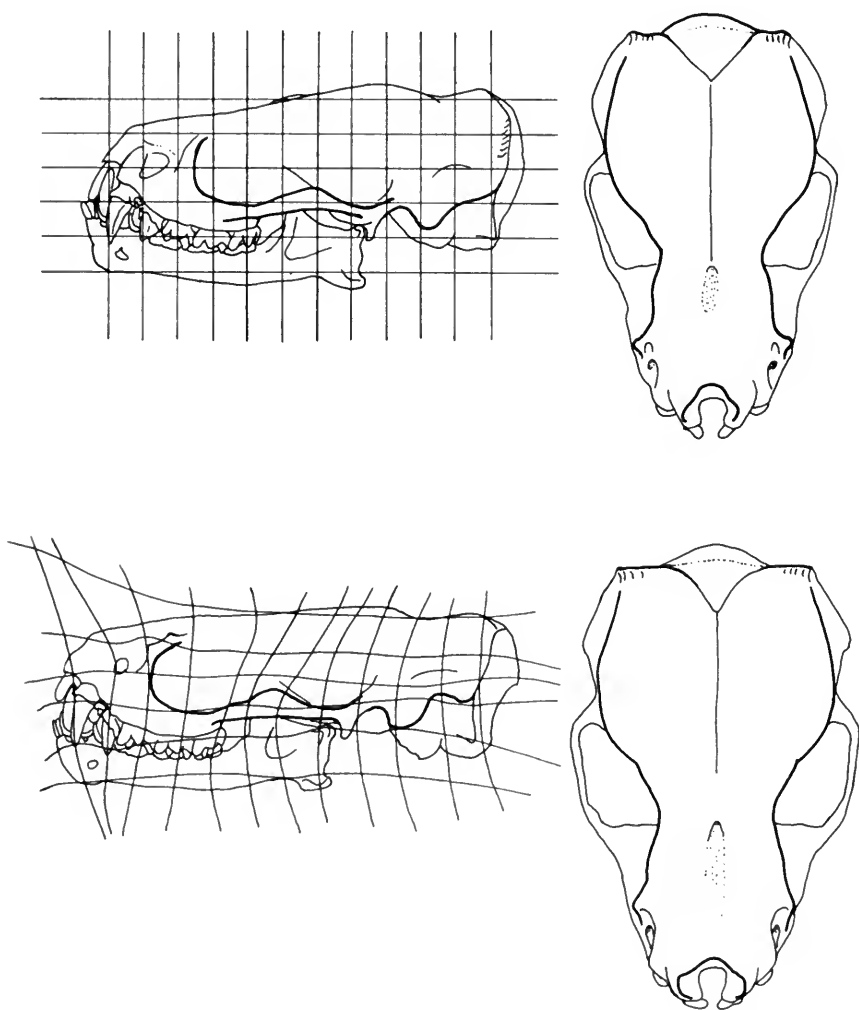


FIG. 23. Pictorial comparison of proportions by regular and deformed coordinates of *Tadarida brasiliensis* (top) from the New World and *Tadarida aegyptiaca bocagei* (bottom) from the Old World. The coordinates are regular for the lateral view of *brasiliensis* and deformed for *aegyptiaca* (for method, see Thompson, 1971; Simpson et al., 1960). The two bats are especially similar from the dorsal view, and coordinates are not drawn.

As to the relationship of the *aegyptiaca-brasiliensis* pair with species of *Mormopterus* and species of *Tadarida*, good evidence exists that they are phenetically similar to each. Indeed, the pair share the same condition of the ears with *Mormopterus*. Next nearest neighbors (size-out distance) of *aegyptiaca* and *brasiliensis* is a New World species of *Mormopterus* and next nearest are species of *Tadarida*. Although a relationship between *brasiliensis* and New World *Mormopterus* has been mentioned by de la Torre (1956) and Handley (1956), *Tadarida brasiliensis* differs by having more wrinkling on the lips and the presence of PM^3 and I_3 (table 11). I suspect the similarity between the *aegyptiaca-brasiliensis* pair and species of *Mormopterus* and *Sauromys* in the flattening of the cranium affects the placement of the pair on the phenogram.

Though in the size-out analysis the *aegyptiaca-brasiliensis* pair averages closer to *Mormopterus* (0.562), it is almost as close to *Tadarida* (0.570). I think the relationship with the latter is substantial. In size-out distance, *brasiliensis* is the nearest neighbor of both *aegyptiaca* and *kuboriensis* and second nearest of *australis*. In correlation, *aegyptiaca* is most highly correlated with *teniotis*, then *brasiliensis*, *fulminans*, and *australis*; and *brasiliensis* is second most highly correlated, after *aegyptiaca*, with *Mormopterus kalinowskii* (table 7). Also, in several of the major morphological characters (table 6), *aegyptiaca* and *brasiliensis* are more in line with the variation in *Tadarida* than in *Mormopterus*.

The largest species of *Mormopterus* joins the cluster at 0.700. *Mormopterus beccarii* (GSL = 18.0 mm) from Australasia is nearest the Malagasy *M. jugularis* (GSL = 16.5 mm) at 0.595, but the nearest neighbor of *jugularis* is actually *norfolkensis* (0.483). The phenetics are slightly distorted here by the phenogram, but the larger or Malagasy forms are more distant from or less similar to the smaller species of *Mormopterus* (table 7). Although Hill (1961) mentioned that *beccarii* is closely related to *planiceps* because of a similar cranial profile and similar development of PM^3 and PM_3 , my analysis does not support that relationship. *Mormopterus beccarii* is one of the most distant species of *Mormopterus*. It is likely that because of its large size, *beccarii* is allometrically out of proportion with other *Mormopterus* for structural reasons intrinsic with its large size. *Mormopterus beccarii* could also be, according to Cope's Rule (see Stanley, 1973), the end of a line of related shapes and not one closely related phylogenetically with the ancestor of the *Mormopterus* line.

Platymops is related phenetically to the *Mormopterus* cluster and joins it at about 0.780 (see also placement in table 6). Nearest neighbors of this flat-headed African bat are *acetabulosus* at 0.673, an African-Malagasy *Mormopterus*; *minutus* at 0.682, a New World form; and *Sauromys* at 0.771, another African flat-headed bat. Peters (1878), who first named the species now called *Platymops setiger*, originally described it as *Mormopterus setiger*. It is the more derived of the two Old World flat-headed bats and other species of *Mormopterus* because PM^3 is lost and the lips appear to be wrinkled and covered with unusually thick hairs (wrinkling was hard to code because of the hairs). A close phylogenetic lineage from a primitive *Mormopterus* via *Sauromys* to *Platymops* is not supported by phenetics. It is more likely that the two flat-headed molossids diverged separately from a primitive *Mormopterus*-like bat. *Platymops* and *Sauromys* are not each other's closest neighbors in the shape analyses, and both are large compared with most species of *Mormopterus*. (*Sauromys* is the nearest size-in neighbor of *Platymops* but at a distance of 0.724; table 7.) I suggest that *Sauromys* and

Platymops be considered subgenera of *Mormopterus*, but they would be the most derived species of the genus.

With the exception of the two species of *Tadarida* attached to this group, all the species of *Mormopterus*, *Sauromys*, and *Platymops* have closest neighbors within the group. Nearest neighboring genera of *Mormopterus* (including *Sauromys* and *Platymops*) are given in Table 8.

Seven bats representing four classical genera (*Molossops*, *Neoplatymops*, *Cynomops*, and *Myopterus*) are assembled in the next cluster (fig. 22). They have been called the conglomerate group in a previous section. On the whole, the cluster is not as dispersed as one might think if, indeed, four genera are involved. These bats tend to have thick dentaries, broad faces, widely separated short, erect and laterally facing ears, no anterior emargination of the palate, and little or no development of wrinkles or basisphenoid pits (table 11; *Myopterus* is an exception in this last trait as it has very deep pits). *Myopterus* and *Neoplatymops* have only medium-narrow wing tips, whereas *Cynomops* has narrow ones and *Molossops* has very broad ones. All are positive on axis II and III and slightly positive on axis IV (fig. 4). I suspect that the larger species of *Myopterus* and *Cynomops* are eating hard items, but less certainty exists for the smaller species, although all have rather thick dentaries.

Based on tooth characteristics, the small *Neoplatymops* has the most primitive condition with four lower incisors, presence of small PM³, and presence of a completely developed posterior commissure on M³. Most derived of the cluster is the African *Myopterus* with only two lower incisors, no PM³, and no posterior ridge on the M³. The two remaining genera, *Molossops* and *Cynomops*, have tooth traits which are between the primitive and advanced states and can to some extent be graded. Although *Molossops* has only two lower incisors and no PM³, it maintains a slight posterior ridge on M³ (of less than one-half length). *Cynomops*, on the other hand, though it has four lower incisors and no PM³, has completely lost the ridge on M³. Goodwin (1958) noted that the incisor number in *Cynomops greenhalli* is variable (two in the male type and four in the female topotype). Warner et al. (1974) presented chromosome data in which *greenhalli* and *abrasus* (*C. brachymeles*?) have 34 chromosomes instead of the primitive number of 48. Also, *Cynomops* contains the largest of the species of *Molossops* and *Cynomops*.

Neoplatymops joins *Molossops* at 0.490. Small and primitive, *Neoplatymops* is distinguished by Peterson (1965) as one of the flat-headed molossids and worthy of generic status. Historically, this bat has been called *Molossops* and *Cynomops*. *Neoplatymops* and *Molossops* are closest neighbors in both shape analyses. The two, relative to all other molossid genera, do not require separate generic status in my study. There are several differences in the teeth and external appearance of these two bats (see Peterson, 1965), but their shape and, I think, habits are basically similar. Not only have the two been thought similar in the past, but 0.490, a relatively low distance, indicates substantial similarity among two bats in my analysis. *Neoplatymops* here is probably more logically classified as a subgenus of *Molossops*.

The three species of *Cynomops* cluster at 0.340, forming a distinct entity. The three join *Neoplatymops*-*Molossops* at 0.610. Species of *Cynomops* are each other's nearest neighbor in both size-out and correlation, but as an entity of three they are nearest (size-out) *Molossops* and *Neoplatymops* (table 8). In the

past, species of *Cynomops* have been called *Molossops*, *Molossus*, *Promops*, and *Myopterus*. *Cynomops* joins *Molossops* at 0.610, and although this number is not a small distance, is about the same as the distance at which other molossid genera form (for example, *Tadarida* and *Otomops*). Peterson (1965) described the differences between *Cynomops* and *Molossops* and considered them to be separate genera, but I think their shapes are similar enough to be included within one genus. Gardner (1977) reported that *Molossops* has 42 chromosomes and differs from the chromosome number of 34 in *Cynomops*. He noted, however, that variation in chromosome number among members of the same molossid genus does occur, for example in *Eumops*. He asked the following question (p. 548): "Does recognition of *Molossops* and *Cynomops* at the generic level better reflect the true relationship between these taxa, or does it obscure their close phylogenetic affinity?" My study does little more to clarify the situation, but relative to other molossid genera already described here, *Molossops* including *Neoplatymops* and *Cynomops*, is about as phenetically dispersed. Subsequently, I list *Cynomops* as a subgenus of *Molossops*.

Neoplatymops, relative to *Molossops* and *Cynomops*, has been described by Peterson (1965, p. 21) as representing an "intermediate condition between *Tadarida* [excluding *Mormopterus*] on the one hand and the *Molossops*-*Cynomops* complex on the other" (based on palate configuration). He suspected that both *Molossops* and *Cynomops* could be derived from *Neoplatymops* because of dental characteristics. Possibly, species of *Cynomops* are the most derived bats of this complex, not so much by tooth criteria but by their narrower wing tips, lower chromosome number, and large-sized species. The largest bat here is *Cynomops brachymeles* which is definitely in a graduated series of similar bats (fig. 17). This large bat could mark the end of this particular *Molossops*-shape line in the New World. The most closely related bats to *Molossops* (*sensu lato*), other than *Myopterus*, in both shape analyses are species of *Mormopterus*, bats with which *Molossops*-like bats share several external morphological features (table 7). Nearest neighboring genera of *Molossops* (plus *Cynomops* and *Neoplatymops*) are listed in Table 8.

The two species of *Myopterus* found only in the Old World, *M. albatrus* (GSL = 23.5 mm) and *M. whitleyi* (GSL = 17.0 mm), join together at a distance of 0.540 units. In the size-out shape analysis the two are more similar to each other than to any other species, but they have a rather high degree of dissimilarity for two species in the same genus. The correlation shape analysis does not make the two closest neighbors. Most highly correlated with the large *M. albatrus* is the large *Cheiromeles parvidens*; most highly correlated with the small *M. whitleyi* is the small *Molossops temminckii*. The correlation coefficient in both instances is low (0.501 and 0.566, respectively), and I suspect general size has affected which bats are neighbors. Likewise, I think the large distance (0.540) between the two species of *Myopterus* is also because of the size difference between the two bats and subsequent allometric changes that even the manipulation of the size-out analysis cannot eliminate. Increase in size has caused structural changes out of proportion with the smaller bat.

Myopterus joins *Molossops*, found only in the New World, at 0.690. The similarity between these Old and New World genera was noted by Miller (1907, p. 246) where he said, "This genus [*Myopterus*], immediately recognizable among Molossine bats by the peculiar form of the lower incisors, more closely re-

sembles the South American *Molossops* than it does any of the known Old World groups." At the time Miller was writing, the species of *Molossops* and *Cynomops* were both included in the genus *Molossops*, and he made an analogy between the large and small species of *Myopterus* and the large *Molossops cerastes* (= *Cynomops brachymeles*) and the small *Molossops temminckii*, the analogy being that the unusual size difference between the two species of *Myopterus* was not unique. My analysis, like Miller's, illustrates that species of great size difference can be closely related phenetically and interpreted as being in the same genus, as in *Myopterus*.

Although similar, I do not put species of *Myopterus* in the same genus with species of *Molossops* (*sensu lato*), but the relatively close morphological resemblance between these two groups is intriguing. *Myopterus*, a derived genus based on dental traits, has no living, close morphological neighbors in the Old World. I suspect *M. albatrus* is the more derived of the two species of *Myopterus* because of its large size.

Myopterus has an unusual morphological character combination that should be mentioned. Most molossids with widely separated ears and unwrinkled lips, features characteristic of most *Mormopterus*-like and *Molossops*-like bats, have shallow basisphenoid pits. These features may indicate a feeding behavior fundamentally different from that of *Tadarida*-like bats. The two species of *Myopterus* have widely separated ears and unwrinkled lips, but they have deep basisphenoid pits, much like those in *Otomops*. I think this peculiar combination further distinguishes *Myopterus* as a distinct genus.

The closest phenetic relatives of *Myopterus*, size-out, are *Molossops temminckii*, then species of *Molossops* (*Cynomops*). I suspect these bats, *Myopterus*, *Molossops*, and *Cynomops*, had a common ancestor, and perhaps *Myopterus* could have had an origin in the New World. The only other African molossids with thick jaws and abbreviated dental pattern, and bats which I suspect eat hard-shelled items as *Myopterus* probably does, are species of *Mops*. It is possible that, with the proliferation of species of *Mops* into nearly all size categories, relatives of *Myopterus* were either squeezed out of existence or speciation in *Myopterus* never got started with the increased competition.

Only four species of *Eumops* make up the next group, but the other three species of that genus are phenetically related to these four and will also be discussed (fig. 22). The four in the immediate group are *E. bonariensis*, *E. underwoodi*, *E. glaucinus*, and *E. maurus*; the more distant forms are *E. hansae*, *E. perotis*, and *E. auripendulus*. Although scattered on the PCA, these seven bats do have a mutual resemblance (fig. 20). The four central species of *Eumops* and *E. hansae* are in the center of the PCA (fig. 4), whereas *perotis* is negative on axis II and *auripendulus* is positive on axis II. All seven bats have four lower incisors, but the posterior ridge on M^3 shows all stages of variability. Only six of the bats have a PM^3 ; and although the specimen of *E. maurus* I studied does not, other specimens of this bat from Suriname do have a small PM^3 (Eger, 1977). The lips of the seven *Eumops* have been coded as finely wrinkled and skirt-like, while the ears of all but *hansae* have been coded for the intermediate condition of joining in a V (this ear condition has definitely been miscoded for *E. perotis* which has well-joined ears). Basisphenoid pits are moderate to deep and wing tips are narrow to very narrow (table 11). The jaw structure and resulting food habits are variable. The large *E. underwoodi* and *E. auripendulus* are thought to

take hard-shelled items and the large *E. perotis*, soft ones. Nothing is known of the food habits of the four smaller species which have medium to thin jaws, but I suspect they take hard and soft items of appropriate size.

The relationship of *E. hansae*, *E. perotis*, and *E. auripendulus* to the four grouped *Eumops* is as follows (table 7): *E. hansae* is nearest *bonariensis* at a size-out distance of 0.690 but most highly correlated with *Tadarida aurispinosa* at 0.353; *E. perotis* is nearest *bonariensis* at a size-out distance of 0.702 and most highly correlated with *E. underwoodi* at 0.795 (surprisingly high); and *E. auripendulus* is nearest in size-out distance to *Molossus bondae* (0.523) but most highly correlated with *glaucinus* (0.714). The remaining four, the grouped species, are closest to one another in size-out and correlation but not always to the same congener (table 7).

Based on dental traits, *Eumops hansae* is probably a more primitive species of *Eumops* because it has a moderately developed PM³, metaconule on M¹, and a completely developed N-cusp pattern on M³, whereas *E. auripendulus* may be a more derived species with a small PM³ and a V-shaped pattern on M³. The other five bats cannot be graded as to primitive and derived dental traits. *Eumops perotis* bears a better developed PM³ than the others, but its M³ has the same degree of development (cusp less than one-half length of second cusp), whereas *E. bonariensis* has a better developed M³ (cusp more than one-half length of second cusp) but a small PM³. The remaining bats bear a small PM³ and a slight posterior cusp on M³ (PM³ in *E. maurus* is variable).

In the phenogram (fig. 22) *bonariensis* joins *underwoodi* at 0.480 and *glaucinus* joins *maurus* at 0.500. These two pairs unite at 0.610. Both *bonariensis* and *underwoodi* are most highly correlated with *perotis*, and while *glaucinus* is most correlated with *underwoodi*, *maurus* is most correlated with *glaucinus*. *Eumops maurus* is the only *Eumops* which has the same neighbor in both shape analyses. There is little or no historical support for these pairings. Sanborn (1932) reviewed the species of *Eumops* and mentioned that the skull of *bonariensis* was similar to that of *glaucinus*, and that *maurus* has a palate like that of *hansae* but is externally like *abrasus* (= *auripendulus*). He did think that *glaucinus* was the most nearly related species to *auripendulus*, a resemblance corresponding to my correlation analysis. Goodwin (1940) named *E. underwoodi* and noted that its skull was shorter and more robust than that of *E. perotis*, and that *underwoodi* really looked like a large *abrasus* (= *auripendulus*). Eger (1977) found, in her analysis using ratios (size is removed), both males and females of *auripendulus* and *underwoodi* paired up first and were then joined by *glaucinus*. Although our analyses are not exactly comparable (she looked at the genus only as an entity and analyzed males and females separately), *auripendulus*, *underwoodi*, and *glaucinus* are species of *Eumops* in my analysis with more robust jaws and skulls (fig. 4).

The more distant species of *Eumops*, except for *hansae*, are associated with other groups: *E. auripendulus* with *Molossus* and *E. perotis* with the *Tadarida-Otomops* complex. *Eumops hansae* is nearest *bonariensis* but correlated with *Nyctinomops aurispinosa*. Sanborn (1932) thought *hansae* was similar to *bonariensis* both in external appearance and in skull shape but that its teeth showed "a strong resemblance to *Tadarida* [including *Nyctinomops*]." When Miller (1902) named the genus *Nyctinomops*, he mentioned that it was intermediate between *Nyctinomus* (Old World *Tadarida*) and *Promops* (including *Eumops*). Drawings comparing the skulls of *hansae* and *aurispinosa* appear in Figures 20 and 15. My

study, as does Eger's (1977), shows *hansae* to be a distant and outlying member of the genus *Eumops*, and if tooth traits are taken into account and the fact that its ears are separated, it is the most primitive species in the genus.

I believe that *auripendulus* appears in the *Molossus* group because both *auripendulus* and *Molossus* have similar jaw and skull characteristics. Both have robust, heavily built skulls (figs. 20, 9). Besides skull characteristics, Brown (1967) found that the baculum of *auripendulus*, a stout rod-shaped bone, could be mistaken for the bacula in species of *Molossus*. As for general skull appearance, *auripendulus* looks more like other species of *Eumops* than like species of *Molossus* (fig. 20), but the fact that *auripendulus* has some of the characteristics of *Molossus*, such as the well-developed sagittal crest and thick dentary, cannot be doubted. I suggest that *E. auripendulus* is convergent with the genus *Molossus* rather than closely related to it phylogenetically.

Eumops perotis is nearest *E. bonariensis* (but at a great distance) and most correlated with *underwoodi* (at a rather high correlation). Other nearest neighbors include several species of *Tadarida* and *Nyctinomops*, with which *perotis* has several jaw and skull features in common. Actually *E. perotis* is a bat of unusually thin jaws for its size (see regressions in a previous section; fig. 7), and I suspect, it is an allometrically enlarged *Eumops* out of proportion with its smaller congeners. Although *perotis* has no baculum, *underwoodi* has one more similar in shape to that in *bonariensis* and *glaucinus* (Brown, 1967). The two large species of *Eumops*, however, do have the same chromosome number of 48 (Warner et al., 1974). In Figure 20 *E. perotis* appears as the largest of a series of similarly shaped species of *Eumops* and, I believe, is only convergent with the *Tadarida*-like genera with which it is associated in the phenogram.

This genus, ironically called *Eumops*, "true molossid," is the most difficult to describe as a particular shape because of its great variation. Historically, species of *Eumops* have been placed in several other genera including *Promops*, *Molossus*, *Myopterus*, and *Tadarida*. My study is no exception in not clearly grouping all the classical species of *Eumops* into one cluster. Because several species are allied morphologically with other clusters, one may wonder if there is a typical *Eumops*-like shape and whether the genus is monophyletic or polyphyletic. I think that species of *Eumops* are monophyletic because of their phenetic similarity in the clustering analyses, their sharing of several derived traits, and their similarity of skull shape. Several forms, however, are convergent toward other ways of molossid life. These convergent forms are the larger species in the genus.

The chromosome work by Warner et al. (1974) and by Dulic & Mutere (1973) presented data on 24 species of molossids. Of these 24, 20 were found to have 48 chromosomes. In the four species of *Eumops* analyzed, *underwoodi* and *perotis* have 48, *auripendulus* has 42, and *glaucinus* has either 40 or 38 (in Colombia and in Chiapas and Costa Rica, respectively). Authors of both papers suggest that 48 is the primitive number of chromosomes for Molossidae. This notion of primitive chromosome number is only partially correlated with the tooth loss configuration in *Eumops*. *Eumops auripendulus* has not only the most derived teeth but also a derived chromosome state. *Eumops glaucinus*, on the other hand, though it has a lower chromosome number, has dental characteristics which are neither derived nor primitive. This last species is grouped with three other species of *Eumops* which make up the cluster of more typical species.

Two species in the distinctive genus *Promops* follow the four species of

Eumops in the phenogram (fig. 20). These two bats are positive on axis II of the PCA (fig. 4), but are not as extreme as *Molossus*. The skull of *Promops*, although shorter and rounder than that of *Molossus*, is not as robust nor is its dentary as thick (fig. 10). Sometimes called the domed-palate bats, species of *Promops* have a distinctive, highly arched palate. These two species have four lower incisors, vestigial PM³, and reduced M³ that has no posterior cusp. Wing tips are narrow, ears join in a V-pattern, lips are unwrinkled, palate is not emarginated, and basisphenoid pits are developed (table 11).

The larger *P. centralis* joins the smaller *P. nasutus* at 0.310. The two are closest neighbors in both shape analyses. *Promops* joins *Eumops* at 0.690. Although the nearest neighbor of both species of *Promops* is a species of *Molossus*, the average distance to the seven species of *Molossus* is greater than the average to the four species of *Eumops*, hence the clustering of *Promops* with the group of four *Eumops*. Most highly correlated neighbors are also *Molossus*. Other authors have remarked on the similarity of *Promops* to *Eumops* and *Molossus*. Miller (1907) stated that *Promops* was intermediate between *Eumops* and *Molossus* but closer to *Molossus*. In dental features, *Promops* does appear intermediate; but in skull features, it is more similar to *Molossus*. Brown (1967) noted that *Promops* has no baculum as is the case in *E. perotis*, but all four species of *Molossus* he examined had at least a small one. *Promops* is also related phenetically to *Molossops temminckii* (size-out distance is 0.704). The two genera, *Promops* and *Molossops*, have several traits in common including relatively thick jaws, unemarginated palate, and unwrinkled lips.

The genus *Molossus* and *Eumops auripendulus* make up the final large cluster of molossids. Because *auripendulus* has already been examined, this discussion concerns itself primarily with traits and relationships of species of *Molossus*. *Molossus* represents an extreme morphological condition for molossids. These bats have thick jaws, well-developed cranial crests, fewer teeth and cusps, and very narrow wing tips (fig. 9, table 6). They are the most positive on axes II and IV and most negative on III in the PCA (fig. 4). There is evidence that species of *Molossus* eat hard-shelled items, such as beetles. All species of *Molossus* have a V-shaped cusp pattern on M³ and have lost PM³ and I₂. They have also nearly lost the lower third premolar, a tooth which is probably being squeezed out by the lower canine and PM⁴. All species of *Molossus* have basisphenoid pits, slightly joined ears, unwrinkled lips, and no palatal emargination (table 11).

Skulls of different species of *Molossus* are difficult to distinguish except for size (fig. 9). Quantitative proof of their similarity can be noted by the fact that five of the species group together before the 0.420 average-least-distance line in Figure 22 and by the high correlation values among all the species (table 7). Although care was taken to use only specimens of distinct species, there may still be misnamed specimens. No recent study has been done which clearly demarcates the species of *Molossus*. The grouping here includes seven OTU's based on 76 measurements and may not agree with the notions of previous authors.

Molossus sinaloae and *M. molossus* form a pair at 0.290. Each is the other's nearest neighbor (table 7), but while *sinaloae* is most highly correlated with *molossus*, the latter is most correlated with *bondae*. It is true that *molossus* and *bondae* are more nearly the same size and *sinaloae* is larger. Hall & Kelson (1959, p. 216) mentioned *M. bondae* as "purportedly resembling *Molossus sinaloae* but smaller," a note which my analysis does not support.

Molossus ater, the largest *Molossus*, joins the *sinaloae*-*molossus* pair at 0.340. The nearest neighbor to *ater* in both shape analyses is *sinaloae*. In the past (Miller, 1913) the larger species of *Molossus*, such as *ater*, *sinaloae*, and *pretiosus*, have been put into a group separate from the groups of smaller species; but more recently (Jones et al., 1971; D. C. Carter, personal communication) groupings of species of *Molossus* have been suggested based on the length and color of the hair. There are two types of hair, long and bicolored (white at base) or short and unicolored (black at base). This analysis does not agree with those groupings based on hair: *M. ater* has short, unicolored hair, while *M. sinaloae* and *M. molossus* have long, bicolored hair. The latter two are, of course, paired (fig. 22).

Molossus bondae and *M. coibensis* pair at 0.250, the lowest distance of any two bats in the study and may represent the same species. These two are also most highly correlated with each other. Historically, the small *M. coibensis* has been thought of as a subspecies of *M. molossus* (Hall & Kelson, 1959; K. F. Koopman, personal communication), and both have long bicolored hair, but the two are not grouped together here. At 0.390 the *bondae*-*coibensis* pair joins *ater*, *molossus*, and *sinaloae*. These five are similar morphologically despite the variation in size. It is a cluster which includes both the largest (*ater*) and the smallest (*coibensis*) species of *Molossus*.

Molossus trinitatus joins the main cluster of species of *Molossus* at 0.470. It is nearest *bondae* in the size-out analysis but more correlated with *sinaloae*. Ojasti & Linares (1971) suggested that *trinitatus* is a subspecies of *sinaloae*. Goodwin (1959), however, noted that this rare bat is not really close to any other *Molossus* but it does have the same long, bicolored hair as *sinaloae*. Brown (1967) reported that the baculum of *M. trinitatus* is longer than that of *sinaloae* and more pointed than that in any other species of *Molossus* he examined. In this analysis *M. trinitatus* is less robust than the other species of *Molossus* in several jaw and skull features and is the species of *Molossus* which is closest to the species of *Promops* in morphology. In my study, I am hesitant to call *trinitatus* a subspecies of any other species of *Molossus*.

The last *Molossus*, *M. pretiosus* joins the cluster at 0.570. In both shape analyses it is closest to *ater*, another large bat. Why *pretiosus* joins at a greater distance is uncertain, but it appears to be distinct from other *Molossus*. Although like *M. ater* in having short, unicolored hair, I agree with Jones et al. (1971) that *M. pretiosus* is not conspecific with *ater* as was stated by Handley (1966).

In my earlier, larger analysis several smaller but questionable species were included as OTU's: *M. barnesi*, *M. lambi*, and *M. pygmaeus*. These three placed sufficiently close to *M. molossus* that I omitted them from my analysis and used only *M. molossus* to represent that particular species. There are no less than eight named, chiefly insular forms originally described as separate species distinct from *M. molossus*. Now most of the forms, both island and mainland, are considered to be synonyms or subspecies of *M. molossus* (see Koopman, 1968; Husson, 1962; Jones et al., 1971).

Two vespertilionid bats, *Nyctalus* and *Mimetillus*, are included in my study to see how close, phenetically, they are to molossids (fig. 22). I chose these two for being molossid-like and not for being typical vespertilionids. Although the phenogram is not as good at representing great distances as it is with smaller ones, it is interesting to note that these two bats appear more phenetically

similar to the main body (they average closer) of molossids than does the genus *Cheiromeles*. *Nyctalus* and *Mimetillus* are each other's nearest neighbor (size-out), but as vespertilionids, they are phenetically closer to the *Mormopterus*-like molossids than to any other group (table 9). Vespertilionids are generally thought of as more primitive than molossids and the similarity of these two species with some of the more primitive molossids is not unexpected. These two do have widely separated ears, no wrinkles, wide anterior palatal emargination, and well-developed M^3 s.

Cheiromeles is the most distinctive genus, morphologically, in the family (fig. 22). The two species are extremely robust molossids with a large body, thick dentaries, wide face and widely separated, short, erect ears, unwrinkled lips, no basisphenoid pits, and broad wing tips. In the PCA *Cheiromeles* occupies a position on the extreme positive end of axes II and III, but it is only slightly negative on axis IV (fig. 4). I suspect that species of *Cheiromeles* eat hard-shelled prey.

Based on tooth reduction, *Cheiromeles* is more derived than *Molossus* because of its functionless PM_3 . Although small in *Molossus*, this tooth is vestigial in *Cheiromeles*. The two genera are most likely similar because of convergent food habits and not because of a close common ancestor. The molossid to which both species of *Cheiromeles* appear phenetically related in the size-out analysis is *Molossops temminckii*, but the two are most highly correlated with *Cynomops brachymeles*. There is some similarity in the shape of the skulls (figs. 17, 19) of these species as well as in the external appearance of the head (widely separated, short, erect ears and unwrinkled lips). Perhaps the *Molossops*-*Cynomops* ancestor mentioned earlier not only started a line that ends in *Myopterus* in Africa but also a line that ends in *Cheiromeles* in the Indo-Malayan region.

Generic Considerations

At or before 0.600 in Figure 22, nine genera form. They are *Nyctinomops* (New World *Tadarida*), *Otomops*, *Chaerephon*, *Mops*, *Molossops*, *Myopterus*, *Promops*, *Molossus*, and *Cheiromeles*. Only *Tadarida*, *Mormopterus*, and *Eumops* do not. The morphological distance or dispersion among species within these three genera is greater than that in the other nine. Also complicating matters is that the method which clusters the species for the phenogram, unweighted pair-group method using arithmetic averages (UPMGA), does not always group OTU's next to its nearest neighbor. Each juncture must be checked in the size-out distance matrix from which the phenogram was taken to see if each OTU has been placed next to or near its nearest neighbor. I believe that 12 natural groups can be discerned in the family because of phenetic similarity, despite the relatively great dispersion in three of the groups.

Specifically, I restrict the genus *Tadarida* to seven Old World and one New World species: *T. teniotis*, *T. africana*, *T. fulminans*, *T. lobata*, *T. australis*, *T. kuboriensis*, *T. aegyptiaca*, and *T. brasiliensis*. The last two are smaller and form a connection with New World molossids. Although all these species of *Tadarida* join together at 0.690 (*T. aegyptiaca* and *T. brasiliensis* average juncture to the group is 0.570), I think they are too similar to be split any further. These eight species form one of the most morphologically dispersed molossid genera.

Species of the genus *Nyctinomops* (formerly species of *Tadarida* from the New World) form a distinct cluster at 0.570 and include *N. aurispinosa*, *N.*

femorosacca, *N. latacaudata*, and *N. macrotis*. Although *Nyctinomops* and *Tadarida* are phenetically similar, there is no one bat that forms a specific connection, not even *T. brasiliensis*, the only species of *Tadarida* in the New World.

Species of *Otomops* form a cluster just before the arbitrary line: *O. martiensseni*, *O. secundus*, *O. wroughtoni*, and *O. papuensis*. These species have the distinctive *Otomops* shape whether large or small. *Otomops* is phenetically related to *Tadarida* through *T. teniotis*.

Species of *Chaerephon* are restricted to medium-sized, *Tadarida*-like bats and form a cluster before the arbitrary line at 0.540. The genus includes *C. ansorgei*, *C. bivitatta*, *C. aloysiisabaudiae*, *C. russata*, *C. major*, *C. nigeriae*, *C. pumila*, *C. chapini*, *C. bemmeli*, *C. plicata*, and *C. johorensis*. With some inconsistency, I add *C. jobensis* to species of *Chaerephon*, and though both shape neighbors are species of *Mops*, it has teeth like those of *Chaerephon*. Until a study with more than one specimen is done I think *jobensis* should remain in *Chaerephon*. *Chaerephon* and *Tadarida* are phenetically related through *C. ansorgei*, *C. bivitatta*, and *C. bemmeli*.

Species of *Mops* form a cluster at 0.570 and consist of small, medium-sized, and large bats, including *M. condylura*, *M. brachyptera*, *M. thersites*, *M. trevori*, *M. niangarae*, *M. congica*, *M. demonstrator*, *M. niveiventer*, *M. midas*, *M. leonis*, *M. nanula*, *M. spurrelli*, *M. mops*, and *M. sarasinorum*. There is a phenetic relationship between *Chaerephon* and *Mops* through *M. condylura* and possibly *C. jobensis*.

Species of the genus *Mormopterus* are more dispersed relatively than most other genera and include the New World *M. (Mormopterus) kalinowskii*, *M. (Mormopterus) minutus*, and *M. (Mormopterus) phrudus*; the Australasian *M. (Mormopterus) lorae*, *M. (Mormopterus) norfolkensis*, *M. (Mormopterus) planiceps*, and *M. (Mormopterus) beccarii*; the African-Malagasy *M. (Mormopterus) jugularis* and *M. (Mormopterus) acetabulosus*; and the African *M. (Sauromys) petrophilus* and *M. (Platymops) setiger*. Some of the morphological dispersion in this genus occurs because I have included *Platymops* in the genus. Although I prefer to lump *Platymops* (distance to nearest neighbor, *Mormopterus acetabulosus*, is 0.673) with species of *Mormopterus*, probably a case could be made to leave it as a monotypic genus. *Mormopterus* is phenetically related to *Tadarida* through *T. brasiliensis* and *T. aegyptiaca* and to several *Molossops*-like bats especially *Molossops (Neoplatymops)*.

Molossops, like *Mormopterus*, includes bats with a variety of tooth configurations, but all are phenetically similar to *Molossops*. *Molossops* includes *M. (Molossops) temminckii*, *M. (Neoplatymops) mattogrossensis*, *M. (Cynomops) brachymeles*, *M. (Cynomops) planirostris*, and *M. (Cynomops) greenhalli*. These bats form a group at 0.610. *Molossops* joins *Myopterus* at 0.690, an Old World genus with which *Molossops* shares many morphological features.

The two species of *Myopterus*, *M. albatrus* and *M. whitleyi*, although like *Molossops*, are distinctive in dental configuration and in the great development of the basisphenoid pits, but the two genera are phenetically related. *Myopterus* is one of the most derived molossid genera and is the most derived of the Ethiopian molossids.

Species of *Eumops*, although a few have some morphological resemblance to other genera, are I think, more similar to one another than to any other group. This genus includes *E. hansae*, *E. bonariensis*, *E. underwoodi*, *E. glaucinus*, *E. maurus*, *E. perotis*, and *E. auripendulus*. There is a phenetic relationship between

Nyctinomops and *Eumops* through *N. aurispinosa* and *E. hansae*. *Eumops* is another of the more morphologically dispersed genera in the family.

The genus *Promops* includes two species, *P. nasutus* and *P. centralis*, and seems intermediate between *Eumops* and *Molossus* phenetically. Although *Promops* is similar to several species of *Eumops*, the genus does have some resemblance with species of *Molossops*.

Bats of the genus *Molossus* form a distinct cluster before the arbitrary line at 0.570 and include *M. ater*, *M. molossus*, *M. sinaloae*, *M. bondae*, *M. coibensis*, *M. trinitatus*, and *M. pretiosus*. These bats are phenetically related to *Promops* through *M. trinitatus*.

Cheiromeles, like *Myopterus*, is phenetically related to *Molossops* in the New World. As large bats, the two species in the genus are greatly out of proportion with any other similar, but smaller, molossid bats. *Cheiromeles* has the most derived dental configuration of any genus in the family.

Even though several of the nine primitive-derived characters (table 11) used to help determine the phyletic relationships have been used in the past by several students of molossid taxonomy (Hill, 1961; Rosevear, 1965; Hayman & Hill, 1971; Peterson, 1965, 1967, 1969, 1971a,b, 1972, 1974; Koopman, 1975), these characters could still be plastic because of functional morphology. Already eliminated are characters related to the development of the sagittal and lambdoidal crests because changes can be seen not only between males and females of a species but also between young and old animals. Characters such as tooth loss, separated ears, lack of basisphenoid pits, unwrinkled lips, and closed palatal emargination, however, may be related to eating beetles and may not be good phylogenetic characters to use. Likewise, the narrowness of a wing tip may have more to do with where a bat lives than to which bat it is related. In other words, many of the nine characters may not be conservative enough to indicate patterns of molossid phylogeny. In Figure 24 I show the cladistic relationships based on only four of the primitive-derived characters: ears, basisphenoid pits, palate, and wrinkles. These four may be less plastic than the other characters concerned with loss of bone or dental material. A summary of all nine characteristics for each genus also appears in Figure 24. I do not think the cladogram gives the whole picture, however, and based on what is now known from the phenetic data, I believe I can present a more complete phylogenetic picture.

Basically, there are two kinds of molossids: those with widely separated ears and those with joined ears. The first dichotomy in the cladogram separates these two groups. The bats with widely separated, short, erect ears usually have shallow or no basisphenoid pits and little or no development of wrinkles on the lips. These bats I call *Mormopterus*-like bats and include *Mormopterus* (with *Sauromys* and *Platymops*), *Molossops* (with *Cynomops* and *Neoplatymops*), *Cheiromeles*, and *Myopterus*.

Mormopterus itself is a genus that has the fewest derived traits. No one species of *Mormopterus* has all the primitive characteristics. Several of these bats do have six lower incisors, the maximum number for chiropterans. In my study it is *Mormopterus* that has a closer phenetic similarity to vespertilionids than any other genus.

Molossops, *Cheiromeles*, and *Myopterus* are separated from *Mormopterus* (fig. 24) because they have no anterior palatal emargination and no wrinkles on the

lips (species of *Mormopterus* are variable in this last trait). Finally, *Myopterus* at the end of this branch is separated from *Molossops* and *Cheiromeles* by having well-developed basisphenoid pits.

As for the more variable primitive-derived traits, all species of *Molossops* have lost I₃ and the metaconule on M¹; *Molossops* (*Molossops*) has lost I₂. All but *M.* (*Neoplatymops*) have lost PM³ and much of the posterior commissure on M³; and the three species of *M.* (*Cynomops*) have narrow wing tips. Phenetically, the more primitive *M.* (*Neoplatymops*) has characteristics that are similar to both *Molossops* and *Mormopterus*.

| Character | <u>Mormopterus</u> | <u>Molossops</u> | <u>Cheiromeles</u> | <u>Myopterus</u> | <u>Tadarida</u> | <u>Chaerephon</u> | <u>Mops</u> | <u>Otomops</u> | <u>Nyctinomops</u> | <u>Eumops</u> | <u>Promops</u> | <u>Molossus</u> |
|-------------------|--------------------|------------------|--------------------|------------------|-----------------|-------------------|-------------|----------------|--------------------|---------------|----------------|-----------------|
| 9 M ³ | - | (+) | + | + | - | - | + | - | - | (+) | + | + |
| 8 M ¹ | - | + | + | + | - | (+) | + | + | + | + | + | + |
| 7 PM ³ | (+) | (+) | + | + | - | - | - | - | - | - | - | + |
| 6 INCISORS | (4) | (4) | 2 | 2 | (4) | 4 | 4 | 4 | 4 | 4 | 4 | 2 |
| 5 WING | - | (+) | - | - | (+) | - | - | - | + | + | + | + |
| 4 WRINKLES | (+) | - | - | - | + | + | + | + | + | + | - | - |
| 3 PALATE | - | + | + | + | - | - | - | - | - | + | + | + |
| 2 PITS | - | - | - | + | (+) | (+) | (+) | + | (+) | + | + | + |
| 1 EAR | - | - | - | - | (+) | + | + | + | + | (+) | + | + |

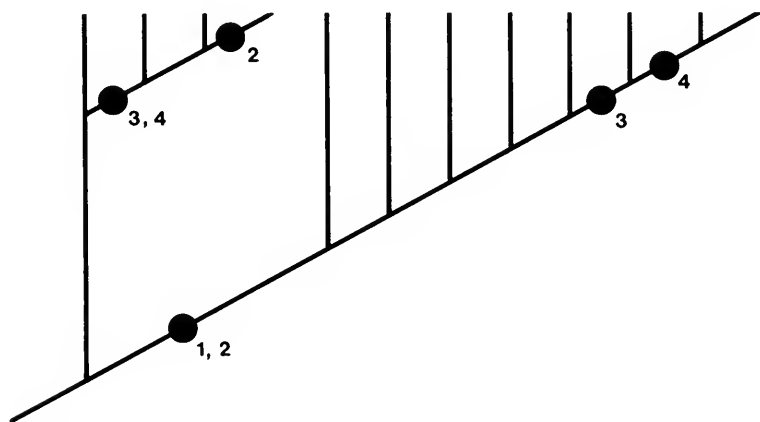


FIG. 24. Summary and cladogram of primitive (-) and derived (+) traits for genera of molossid bats. When a genus has species with both states, the symbol is circled. Traits for each species are listed in Table 11. The cladogram is aligned with the columns in the table. A line is drawn after the first four characters on which the cladogram is based (see text for explanation).

Like *Molossops*, *Cheiromeles* and *Myopterus* have both lost teeth so that each has the most derived molossid dental formula. Data from my phenetic study suggest that *Myopterus* and *Cheiromeles* are related to *Molossops*.

The bats remaining on the right-hand branch of the cladogram (fig. 24) are bats with large, slouched ears, well joined over the nose or ears intermediate in size and just joining over the nose and some development of the basisphenoid pits. These, I think, are *Tadarida*-related molossids and include *Tadarida* (both hemispheres), *Chaerephon*, *Mops*, and *Otomops* in the Old World; and *Nyctinomops*, *Eumops*, *Promops*, and *Molossus* in the New World.

Tadarida, like *Mormopterus*, has species with few derived characters and two species, *Tadarida teniotis* and *T. brasiliensis*, have the greatest number of teeth (32) of all molossids (but not the maximum for Chiroptera, which is 38). A close phylogenetic relationship may exist between *Tadarida* and *Mormopterus* because *T. brasiliensis* and *T. aegyptiaca* have been placed close to species of *Mormopterus* phenetically (fig. 22).

In the four more conservative characters from which the cladogram was composed, *Tadarida*, *Chaerephon*, *Mops*, *Otomops*, and *Nyctinomops* share the same derived traits, namely large, slouched ears joined over the nose, development of the basisphenoid pits (though this is a variable trait among species), and wrinkled lips. There are some differences, however, in the more variable traits. With *Chaerephon* and *Mops* there is change in the tooththrow toward a more derived state, particularly in *Mops*, and several species of both genera have a palatal emargination that is nearly closed. Neither *Chaerephon* nor *Mops* have species with narrow wing tips as do some species of *Tadarida*. *Otomops* and *Nyctinomops* share many of the same derived characters with *Tadarida*, but the characters seem to be amplified. All species of *Otomops* have deep basisphenoid pits and all species of *Nyctinomops* have very narrow wing tips. The phenetic data suggest possible phylogenetic relationships between *Tadarida* and *Chaerephon* and between *Chaerephon* and *Mops*, between *Tadarida* and *Otomops*, and between *Tadarida* and *Nyctinomops*.

The next genus, *Eumops*, has, for the most part, the derived condition for all four of the less variable traits in Figure 24. Nearly all the species of *Eumops* have joined ears, basisphenoid pits, closed anterior palate, and fine wrinkles on the lips (*E. hansae* is coded for having separated ears). Just past *Eumops* in the cladogram are *Promops* and *Molossus*, genera which I think have had a reversal in the wrinkles on their lips. These three genera, *Eumops*, *Promops*, and *Molossus*, are more derived than *Tadarida* because they all have narrow wing tips and some abbreviation of the teeth (*E. hansae* is the only exception). The three have more derived characters than any of the other molossid genera, and *Molossus* has the most derived tooththrow of any *Tadarida*-related genus. The phenetic data suggest *Eumops* has some relationship to *Nyctinomops*, and *Molossus* is closely related to *Promops*. Although I am less sure about the phylogenetic relationship between *Promops* and *Molossus* with other molossid genera, *Promops*, after *Molossus*, is phenetically nearer four species of *Eumops* and next closest to species of *Molossops*. Cladistically, the ears, although shorter, are more like those of *Eumops* and other *Tadarida*-related bats rather than those of *Molossops*; hence the placement of *Promops* in the cladogram.

In conclusion, I think there are two major groups of molossids based on ear design. Within each group, parallel trends occur which are probably related to

two basically different methods of detecting and consuming prey. Within the *Mormopterus* groups there are bats that have gracile skulls and jaws with the more primitive tooththrow configuration (*Mormopterus* [*Mormopterus*], *Molossops* [*Neoplatymops*]) and bats with robust skulls and jaws that tend to lose teeth (*Molossops* [*Cynomops*], *Myopterus*, *Cheiromeles*). Likewise, in the *Tadarida* groups, *Tadarida*, *Chaerephon*, *Otomops*, *Nyctinomops*, and some species of *Eumops* have less robust skulls and *Mops*, *Eumops* (part), *Promops*, and *Molossus* have more robust skulls and some abbreviation of the tooththrow.

Geographic Considerations

Is there any pattern to how molossids diversified morphologically in different areas? What is the composition of each fauna in terms of primitive and derived molossids? What fauna might be the oldest?

This last section is an extension of the Ecology section in that I infer the ecological structure of each molossid fauna from the morphological structure. For this reason, the distance values used here include the size of the bats. Findley (1975) has done a similar study but of a total bat community.

A simple way to look at the morphological dispersion of a fauna, statistically, is to determine each bat's average distance (\bar{d}) to every other bat in that fauna, to sum the averages, and to take the faunal average ($\bar{\bar{d}}$). The average distance for each bat tells how close an individual bat is from every other bat in the particular fauna (see Findley, 1975). A low average indicates that the bat is phenetically similar to most of the bats in the fauna, and a high \bar{d} value indicates that the bat is more distinct phenetically (more unusual morphologically) and is farther away from other members of the fauna. In detecting the highly distinctive taxa in each fauna, I can give some idea of which bats are affecting the morphological dispersion; and by calculating the $\bar{\bar{d}}$ for each fauna, I can compare the dispersions in each fauna.

The bats in all three faunas and their average distance to their faunal neighbors are listed in Table 12. By the Kruskal-Wallis nonparametric test, a very significant difference ($p < .001$) occurs among the $\bar{\bar{d}}$ values of the three faunas, but exactly which faunas are significantly different presents a statistical problem. Because there is no nonparametric multiple range test to handle unequal sample sizes, a Mann-Whitney U test was run on all combinations of two of the three faunas. The Indo-Australian fauna is more dispersed than the Ethiopian and the Neotropical faunas at very significant levels ($p = .0001$ and $p = .0004$, respectively). The Neotropical fauna is more dispersed than the Ethiopian fauna but at a lower level of significance ($p = .0238$).

The distributions of the averages in each fauna are shown in Figure 25. Ethiopia contains several bats with relatively low \bar{d} values, lower than in either of the other two faunas, and several bats with only moderately high values, like *Otomops martiensseni*, *Mops midas*, and *Tadarida africana*. The bats in this fauna are the least dispersed of the three and have the least morphologically distinctive molossids.

Molossids in the Neotropical fauna have no members with averages as low as those in the Ethiopian and contain two bats with averages higher than the highest ones in Ethiopia. This second fauna is not only more dispersed statistically than the first, but it also contains the distinctly different molossids, *Eumops perotis* and *E. underwoodi*.

TABLE 12. Average distance (\bar{d}) of each molossid bat to every other bat in its respective fauna. The means for each fauna (\bar{d}) are significantly different by a Kruskal-Wallis non-parametric test ($p = .000001$). More specifically, the Mann-Whitney U test shows that the Indo-Australian fauna is significantly different from the Ethiopian ($p = .0001$) and Neotropical ($p = .0004$) faunas; and the Neotropical fauna is significantly different from the Ethiopian fauna ($p = .0238$).

| Ethiopia | \bar{d} | Neotropics | \bar{d} | Indo-Australia | \bar{d} |
|-----------|-----------|------------|-----------|----------------|-----------|
| T AEGYPA | .986 | T AURISA | 1.130 | T TENIOA | 1.375 |
| T AFRICA | 1.435 | T BRASIA | 1.196 | T AUSTRA | 1.422 |
| T FULMIN | 1.110 | T FEMORA | 1.171 | T KUBORI | 1.304 |
| T LOBATA | 1.173 | T LATICA | 1.055 | TC JOHOR | 1.229 |
| T ANSORA | .884 | T MACROA | 1.372 | TC PLICA | 1.219 |
| TC ALOYA | .927 | TR KALIN | 1.294 | TC JOBEN | 1.248 |
| TC BIVIA | .868 | TR MINUA | 1.432 | TM MOPSA | 1.215 |
| TC BEMMI | .928 | TR PHRUD | 1.205 | TM SARSA | 1.290 |
| TC CHAPI | 1.221 | E AURIPA | 1.411 | TR BECCR | 1.459 |
| TC MAJOR | .904 | E BONARA | 1.009 | TR LORIA | 1.599 |
| TC NIGEA | .894 | E GLAUCA | 1.354 | TR NORFA | 1.491 |
| TC PUMIA | .925 | E HANSAE | 1.151 | TR PLANA | 1.498 |
| TC RUSSA | 1.017 | E MAURUS | 1.058 | OTO PAPU | 1.306 |
| TM BRACH | .941 | E PEROTA | 2.280 | OTO SECA | 1.366 |
| TM CONDA | .996 | E UNDERA | 2.035 | OTO WROA | 1.443 |
| TM CONGA | 1.377 | MP TEMMA | 1.367 | C PARVID | 2.826 |
| TM DEMOA | .939 | CP BRACA | 1.180 | C TORQUT | 2.747 |
| TM LEONA | .999 | CP GREEA | 1.074 | - | |
| TM MIDAA | 1.652 | CP PLANA | 1.176 | \bar{d} | 1.532** |
| TM NANUA | 1.201 | NEOPLATA | 1.379 | s | .471 |
| TM NIANG | 1.182 | M ATERA | 1.196 | | |
| TM NIVEI | .962 | M BONDAA | 1.020 | | |
| TM THERA | .952 | M COIBEA | 1.168 | | |
| TM TREVO | 1.172 | M MOLOSS | 1.096 | | |
| XIPHONYC | 1.288 | M PRETIA | 1.205 | | |
| TR ACETA | 1.336 | M SINALA | 1.043 | | |
| TR JUGUA | 1.150 | M TRINIT | 1.014 | | |
| MYOP ALB | 1.353 | PRO CENA | 1.062 | | |
| MYOP WHA | 1.129 | PRO NASU | 1.042 | | |
| OTO MARA | 1.606 | - | | | |
| PLATYMOP | 1.262 | \bar{d} | 1.247* | | |
| SAUROMYS | 1.092 | s | .280 | | |
| - | | | | | |
| \bar{d} | 1.121 | | | | |
| s | .207 | | | | |

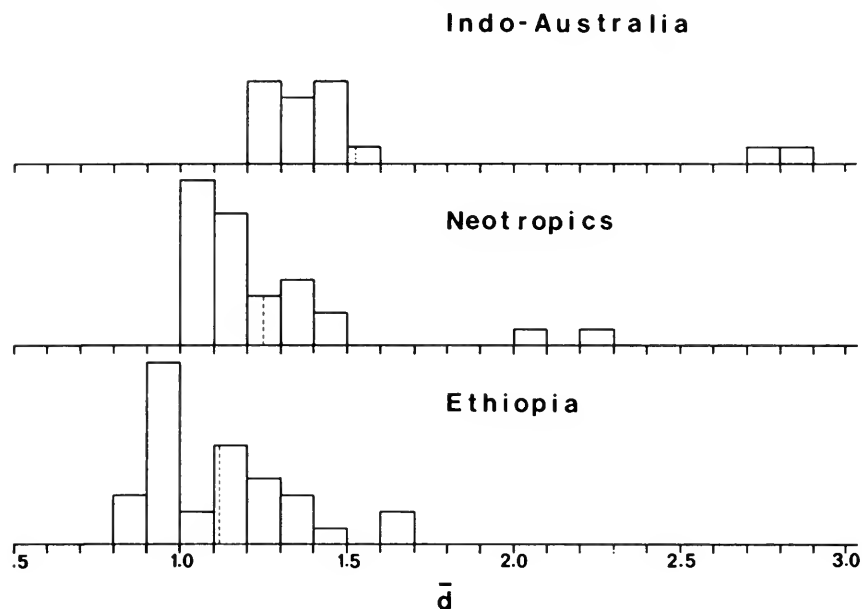


FIG. 25. Distribution of average distances (\bar{d}) in three molossid faunas. The dashed line in each figure represents the mean value (\bar{d}) for that fauna. A list of \bar{d} values is given in Table 12.

The third fauna, the Indo-Australian, contains molossids even more dispersed than those in the Neotropics and has the most highly distinctive taxa of any molossid fauna, namely *Cheiromeles parvidens* and *C. torquatus*.

Findley (1972, 1975) reasoned that the more phenetically diverse a fauna, the older it is; hence, in this analysis the Indo-Australian fauna would be the oldest; the Neotropical, next oldest; and the Ethiopian, the youngest. Probably a good case can be made for this arrangement, including the idea that *Cheiromeles* is the remnant of an ancient molossid fauna. The Indo-Australian fauna is depauperate of molossid species compared to the other two faunas. Coincidentally, and perhaps importantly, two species of echolocating swiftlets (*Collocalia*) occur in this region, and Fenton (1975) suggested that possible competition with these birds helped to make or keep the fauna depauperate of molossids. If so, maybe the presence of the birds helped to disperse the molossid fauna morphologically as well.

A second case can be made for the oldest molossid fauna being the Ethiopian. This fauna contains the greatest concentration of molossids which are most similar phenetically and the least dispersed of the three faunas. Not only have more species evolved in the Ethiopian fauna, but they have also radiated into more ecological roles (table 10). There are presently both small and very large moth eaters and small and very large beetle eaters, roles filled by ecologically diverse but relatively primitive molossids. The majority of species are *Tadarida*-related bats. The Indo-Australian and Neotropical faunas are more diverse phenetically, but the first lacks a very large moth-eater and the second, a very large beetle-eater. I think the very large bats in each of these faunas repre-

sent examples of ecological release into unique niches where no competition has occurred for some time.

Still a third case can be made for the Neotropical region having the oldest fauna because it has the most derived genera, *Eumops*, *Promops*, and *Molossus*; based on the nine primitive-derived traits. Among these derived genera are species specialized for moth diets and species specialized for beetle diets. Also the Ethiopian *Myopterus* and the Indo-Australian *Cheiromeles* are phenetically related to *Molossops* in the New World; *Tadarida aegyptiaca* and *T. brasiliensis* are related and *T. brasiliensis* may be the most primitive living molossid; and the more derived species of *Mormopterus* are in the New World while their close phenetic neighbors are in both Ethiopia and Indo-Australia. This fauna of the New World contains a large concentration of *Mormopterus*-related bats.

SUMMARY

The primary goal of my study, determining natural morphological groups of molossid bats, is accomplished by defining exactly the variation which occurs among the extant molossid species. I attempted to include as many of the species in the family as was possible.

To do this, I used principal components, distance (size-in and size-out), and correlation analyses on 80 species. Morphological trends that emerge from the data are size, as indicated by the first component; a suite of jaw characters, by the second; several facial features, by the third; and a few less important features, but particularly a wing characteristic, by the fourth. Each of the groups of phenetically similar molossids which appear in the PCA and in the distance and correlation analyses are described in terms of characters which are most highly correlated with the components. In particular, the second component, concerned with jaw structure, divides the species in the following way: *Cheiromeles*, *Molossus*, *Promops*, *Mops*, *Myopterus*, *Molossops* (including *Neoplatymops* and *Cynomops*), and several species of *Mormopterus* (including *Platymops*) and *Eumops* are located on the positive side of this axis, meaning these molossids have relatively thick jaws and robust skulls; molossids on the negative side, *Tadarida*, *Nyctinomops*, *Chaerephon*, *Otomops*, and several species of *Mormopterus* (including *Sauromys*) and *Eumops*, have thin jaws and less robust skulls. I use the suite of jaw characters to predict what molossids are eating and give data to support the predictions: bats with thick jaws eat hard-shelled insects like beetles, and bats with thin jaws eat soft-shelled insects like moths. Likewise, I predict where molossids may be roosting or flying based on the shape of their wing tips. Bats with broad (relative to other molossids) wing tips may be slower and more maneuverable than molossids with narrow tips, and the few data available support this notion. Molossids tend to have two kinds of appearances: one with large, anteriorly directed ears which are joined over the nose, lips that are wrinkled, and basisphenoid pits that are medium or deep; and the other with short, laterally directed ears which are widely separated, lips that are unwrinkled, and basisphenoid pits that are shallow or nonexistent. I suspect that the two different appearances indicate two different ways in which molossids detect and consume prey, but I have no data to support or refute this thought.

Ecologically, both New and Old Worlds contain molossids with thick and thin jaws, *Molossus* in the New World and *Mops* in the Old World are probably

ecological counterparts in that both probably concentrate on hard-shelled foods. The same is true of several molossids with thin jaws in both the New and Old Worlds; these bats are probably concentrating on soft-shelled prey. However, in another morphological characteristic, the width of the wing tip, the fauna in the New World contains most of the species with narrow wing tips. As for general size in molossids, the percentage of medium-sized bats is approximately the same in both New and Old Worlds; but the Old World tends to have a greater percentage of large molossids, whereas the New World has a greater percentage of small ones.

The evolutionary or phylogenetic relationships among the species and the genera are examined phenetically and with the use of several primitive-derived characters. Twelve genera are delineated:

Chaerephon (formerly *Tadarida* [*Chaerephon*])

Cheiromeles

Eumops

Molossops (including *Neoplatymops* and *Cynomops* as subgenera)

Molossus

Mops (formerly *Tadarida* [*Mops*]; includes *Xiphonycteris*)

Mormopterus (formerly *Tadarida* [*Mormopterus*]; including *Sauromys* and *Platymops* as subgenera)

Myopterus

Nyctinomops (including four New World species formerly assigned to *Tadarida*)

Otomops

Promops

Tadarida

Three of these genera, *Tadarida*, *Mormopterus*, and *Eumops*, are more dispersed morphologically than the other nine. I think all 12 form natural groups based on morphological similarity.

In terms of primitive-derived traits, two groups emerge: the *Mormopterus*-like bats and the *Tadarida*-like bats. *Tadarida* and *Mormopterus* are the two most primitive genera to which all other genera can be related. The two groups differ primarily in ear design, separated or joined, and associated characters mentioned above and represent two basically different ways of detecting and consuming prey. Parallel trends of tooth loss and increased robustness of the skull occur in both groups. Genera in the *Mormopterus* group are *Mormopterus*, *Molossops*, *Myopterus*, and *Cheiromeles*; and genera in the *Tadarida* group are *Tadarida*, *Nyctinomops*, *Chaerephon*, *Mops*, *Otomops*, *Eumops*, *Promops*, and *Molossus*. These last three genera are the most derived in the family.

Geographically, the Indo-Australian molossid fauna is the most dispersed morphologically followed by the Neotropical and Ethiopian faunas. Good cases can be made for all three being the oldest molossid fauna: morphologically, the most distinctive genus, *Cheiromeles*, is found in the Indo-Australian fauna; ecologically, the Ethiopian molossids seem to fill more completely the available niches; and phylogenetically, the most derived genera are in the New World.

APPENDIX A

Data for 76 characters for each of 80 OTU's. Abbreviations are in Materials and Methods section.

| | | | | | | | | | | | | | | | | | | | | |
|-----------|---|--------|---|---------|---|--------|---|--------|---|--------|---|--------|---|--------|---|--------|---|--------|---|--------|
| HEAD BOO | T | AEGYPA | T | AFRICA | T | ANSORA | T | AURISA | T | AUSTRA | T | BRASIA | T | FENDRA | T | FULMIN | T | KUSBRI | T | LATICA |
| TAIL | | 44:000 | | 104:000 | | 34:000 | | 74:000 | | 84:000 | | 67:000 | | 62:000 | | 84:000 | | 89:000 | | 58:000 |
| EAR | | 17:000 | | 61:000 | | 21:000 | | 41:000 | | 48:000 | | 37:000 | | 42:000 | | 51:000 | | 41:000 | | 38:000 |
| HF | | 16:000 | | 28:000 | | 19:000 | | 5:000 | | 28:500 | | 16:000 | | 2:200 | | 10:000 | | 12:000 | | 18:000 |
| TIBIA | | 13:200 | | 20:000 | | 13:500 | | 13:400 | | 17:400 | | 12:500 | | 13:400 | | 16:700 | | 15:000 | | 12:300 |
| FOREARM | | 10:200 | | 64:000 | | 45:300 | | 50:000 | | 58:200 | | 42:500 | | 40:600 | | 58:000 | | 58:200 | | 45:000 |
| 3 MEAL | | 20:000 | | 54:000 | | 19:600 | | 31:300 | | 22:200 | | 16:400 | | 18:000 | | 23:000 | | 23:000 | | 15:000 |
| 3M 2PHAL | | 17:000 | | 18:400 | | 17:800 | | 18:400 | | 22:200 | | 14:700 | | 17:200 | | 23:000 | | 23:000 | | 15:000 |
| 4 MEAL | | 47:000 | | 62:000 | | 44:600 | | 18:200 | | 25:500 | | 12:700 | | 17:500 | | 17:600 | | 15:000 | | 12:500 |
| 4M 2PHAL | | 16:200 | | 21:000 | | 16:000 | | 23:600 | | 17:500 | | 13:500 | | 2:400 | | 32:400 | | 15:100 | | 20:000 |
| 5 MEAL | | 18:100 | | 38:000 | | 17:300 | | 25:000 | | 34:500 | | 28:200 | | 1:000 | | 10:100 | | 13:200 | | 13:700 |
| 5M 2PHAL | | 30:000 | | 17:000 | | 13:000 | | 7:000 | | 10:800 | | 13:200 | | 1:000 | | 17:000 | | 18:400 | | 13:000 |
| 5M 2PTIP | | 14:200 | | 11:000 | | 9:400 | | 11:000 | | 11:000 | | 15:000 | | 9:000 | | 17:000 | | 12:000 | | 9:000 |
| 3M TIP | | 7:600 | | 19:000 | | 8:400 | | 2:200 | | 14:000 | | 12:500 | | 2:600 | | 4:000 | | 4:000 | | 5:000 |
| UP CANIN | | 3:500 | | 4:000 | | 9:100 | | 2:500 | | 27:000 | | 12:500 | | 1:000 | | 23:200 | | 21:400 | | 19:100 |
| GSN INCI | | 10:500 | | 24:000 | | 18:500 | | 25:600 | | 27:600 | | 16:000 | | 1:000 | | 22:000 | | 21:400 | | 17:100 |
| COST INCI | | 19:000 | | 24:000 | | 17:800 | | 9:000 | | 2:000 | | 17:000 | | 1:200 | | 1:500 | | 8:400 | | 5:400 |
| ROST LEM | | 16:400 | | 9:000 | | 17:000 | | 9:000 | | 8:500 | | 5:000 | | 1:200 | | 8:500 | | 0:0 | | 5:000 |
| LACR WID | | 7:400 | | 9:000 | | 6:600 | | 9:400 | | 6:400 | | 4:000 | | 1:200 | | 15:300 | | 15:700 | | 12:000 |
| INTORB | | 5:800 | | 17:000 | | 4:000 | | 13:500 | | 16:700 | | 10:500 | | 1:800 | | 15:000 | | 15:700 | | 12:000 |
| CON CANI | | 13:300 | | 10:000 | | 12:000 | | 6:300 | | 3:600 | | 16:000 | | 1:800 | | 9:300 | | 9:700 | | 17:000 |
| LORECHTR | | 11:200 | | 10:000 | | 1:600 | | 1:200 | | 1:200 | | 1:100 | | 1:200 | | 1:300 | | 1:400 | | 1:200 |
| TR ECHTIC | | 1:600 | | 2:000 | | 1:000 | | 1:200 | | 1:600 | | 1:300 | | 1:000 | | 1:600 | | 2:000 | | 1:200 |
| DEMT COR | | 3:800 | | 4:000 | | 1:500 | | 1:600 | | 5:100 | | 1:300 | | 1:800 | | 4:500 | | 4:500 | | 3:500 |
| MONI ANG | | 3:600 | | 3:000 | | 3:500 | | 3:500 | | 3:700 | | 2:000 | | 3:000 | | 5:100 | | 5:500 | | 3:800 |
| POST ORB | | 12:000 | | 5:000 | | 4:100 | | 1:200 | | 15:800 | | 9:000 | | 1:600 | | 17:800 | | 14:300 | | 10:800 |
| ZYG ORB | | 10:600 | | 12:000 | | 1:600 | | 1:200 | | 12:800 | | 8:100 | | 1:600 | | 1:200 | | 1:600 | | 10:800 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | 1:200 | | 13:000 | | 12:400 | | 10:000 |
| SCAS ORB | | 11:000 | | 14:000 | | 10:700 | | 1:200 | | 13:600 | | 9:000 | | | | | | | | |

| | T AEGYPA | T AFRICA | T ANSORA | T AURISA | T AUSTRA | T BRASIA | T FEMORA | T FULMIN | T KUBCRI | T LATICA |
|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| M3 M3 | 4900 | 9200 | 5000 | 4800 | 5800 | 3700 | 4200 | 5400 | 000 | 4200 |
| ANTPIER | 3000 | 2400 | 2000 | 4800 | 3100 | 2200 | 1900 | 2300 | 2600 | 1900 |
| POSTPIER | 3000 | 2700 | 2000 | 3000 | 4300 | 2400 | 2800 | 3200 | 3400 | 2400 |
| LOCANIN | 3300 | 4600 | 2900 | 2900 | 3800 | 2000 | 2800 | 3800 | 000 | 2400 |
| DEFORANT | 14000 | 17900 | 12900 | 14500 | 17200 | 11400 | 13200 | 16000 | 13400 | 10800 |
| FORANT | 12100 | 14900 | 11000 | 12500 | 14600 | 9800 | 11200 | 13400 | 13400 | 10800 |
| ANGUL L | 2700 | 3600 | 2800 | 4300 | 3400 | 2200 | 2600 | 3100 | 3600 | 2300 |
| CDN CORO | 4000 | 5100 | 3300 | 4300 | 5400 | 3000 | 3600 | 4700 | 4500 | 3600 |
| CONO MI | 10200 | 12600 | 9400 | 10400 | 12800 | 8400 | 9800 | 11700 | 11500 | 9000 |
| ANGUL W | 12300 | 3200 | 2200 | 4800 | 2600 | 1800 | 2400 | 2700 | 2800 | 2000 |
| CORO MT | 4000 | 4600 | 3200 | 3600 | 4200 | 3100 | 2800 | 4200 | 4600 | 3200 |
| INCIFOR | 4000 | 4000 | 3000 | 3000 | 4000 | 4000 | 3000 | 4000 | 4000 | 3000 |
| INSHAP | 3000 | 3000 | 3000 | 1000 | 2000 | 1000 | 1000 | 3000 | 1000 | 1000 |
| PREMOLAR | 3000 | 2000 | 3000 | 4000 | 2000 | 2000 | 1000 | 4000 | 1000 | 1000 |
| BASI PIT | 1000 | 4000 | 2000 | 1000 | 2000 | 1000 | 1000 | 3000 | 1000 | 1000 |
| P SAGITT | 1000 | 1000 | 2000 | 2000 | 1000 | 1000 | 1000 | 3000 | 1000 | 1000 |
| SAGITT | 1000 | 1000 | 1000 | 2000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| ER JUNC | 1000 | 1000 | 1000 | 2000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| WINKLES | 3000 | 2000 | 2000 | 2000 | 3000 | 3000 | 2000 | 4000 | 2000 | 2000 |
| MI META | 3000 | 2000 | 2000 | 2000 | 3000 | 3000 | 2000 | 4000 | 2000 | 2000 |
| GLENO L | 1800 | 2400 | 1800 | 2200 | 2400 | 1600 | 1700 | 2000 | 2000 | 2000 |
| GLENO V | 1900 | 3000 | 1900 | 2200 | 2800 | 1600 | 1700 | 2000 | 2000 | 2000 |
| CONOY L | 1400 | 2300 | 1400 | 2100 | 2800 | 1600 | 1700 | 2000 | 2000 | 2000 |
| UP MOL R | 5500 | 6700 | 5100 | 1400 | 6600 | 4700 | 1500 | 1900 | 1800 | 1800 |
| MAIRNES | 2000 | 2000 | 2000 | 2000 | 3000 | 2000 | 1000 | 2000 | 2000 | 2000 |
| L LAMBOO | 1000 | 3000 | 2000 | 2000 | 2000 | 2000 | 1000 | 3000 | 2000 | 2000 |
| DIGIT 3 | 94400 | 12000 | 92000 | 96000 | 11800 | 83700 | 91300 | 11800 | 114200 | 86000 |
| DIGIT 4 | 2100 | 91700 | 70900 | 96000 | 89900 | 45700 | 46800 | 83000 | 88000 | 46000 |
| DIGIT 5 | 50800 | 67700 | 47400 | 50400 | 60900 | 45100 | 46100 | 55000 | 58000 | 46000 |
| ASPECT | 2827 | 2783 | 2903 | 2976 | 2847 | 2700 | 2965 | 2915 | 2971 | 2550 |
| TIP IND | 65700 | 65800 | 66800 | 66690 | 66210 | 65600 | 66790 | 65700 | 66281 | 65750 |
| D3 I DS | 1858 | 1832 | 1943 | 1938 | 1885 | 1835 | 1980 | 1911 | 1969 | 1866 |
| EM I FA | 0346 | 0435 | 0441 | 0517 | 0486 | 0355 | 0467 | 0426 | 0361 | 0351 |
| COMIT DL | 0114 | 0080 | 0109 | 0083 | 0070 | 0066 | 0091 | 0094 | 0068 | 0105 |
| COMIT DL | 0100 | 0111 | 0083 | 0083 | 0093 | 0080 | 0083 | 0112 | 0080 | 0105 |
| M1+M2 DL | 0314 | 0554 | 0551 | 0520 | 0512 | 0529 | 0515 | 0525 | 0541 | 0556 |
| COR H | 0286 | 0274 | 0248 | 0250 | 0244 | 0272 | 0212 | 0262 | 0302 | 0258 |

| MEAC 800 | TC NIGEA | TC PLICA | TC PUNIA | TC RUSSA | TM BRACH | TM CONDA | TM CONGA | TM DEMOA | TM LEGNA | TM MIAA |
|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|---------|
| TAIL | 70.500 | 67.500 | 64.500 | 60.700 | 0.0 | 84.000 | 69.500 | 70.000 | 95.000 | 101.500 |
| EAR | 30.500 | 36.500 | 33.500 | 31.500 | 70.000 | 44.000 | 38.500 | 35.000 | 35.000 | 41.500 |
| HF | 18.500 | 17.500 | 18.000 | 19.500 | 15.000 | 17.000 | 24.000 | 18.000 | 19.500 | 27.500 |
| TIBIA | 10.800 | 9.200 | 10.000 | 9.400 | 8.700 | 11.300 | 13.000 | 8.400 | 11.500 | 17.500 |
| FOREARM | 14.800 | 13.700 | 12.200 | 13.600 | 9.000 | 13.700 | 15.400 | 1.500 | 1.200 | 17.500 |
| 3 META | 42.800 | 45.500 | 41.000 | 42.000 | 36.700 | 46.000 | 45.100 | 4.500 | 35.500 | 61.500 |
| 3M 1PHAL | 45.800 | 46.400 | 47.500 | 46.600 | 40.200 | 47.800 | 57.500 | 4.200 | 37.500 | 62.500 |
| 3M 2PHAL | 18.900 | 17.100 | 17.000 | 20.000 | 16.500 | 21.000 | 25.600 | 1.200 | 13.500 | 25.500 |
| 4 META | 44.600 | 44.200 | 40.800 | 45.400 | 39.200 | 46.500 | 22.500 | 1.300 | 36.100 | 61.500 |
| 4M 1PHAL | 14.300 | 14.300 | 14.300 | 15.400 | 13.800 | 17.600 | 21.800 | 1.500 | 11.500 | 20.500 |
| 5 META | 15.800 | 10.800 | 11.800 | 10.600 | 11.200 | 15.800 | 10.800 | 1.900 | 8.400 | 16.700 |
| 5M 1PHAL | 28.200 | 26.900 | 27.000 | 28.300 | 26.800 | 32.000 | 32.400 | 2.400 | 24.400 | 37.000 |
| 5M 2PHAL | 14.000 | 14.000 | 13.000 | 13.000 | 10.300 | 13.200 | 15.800 | 1.600 | 9.600 | 17.400 |
| 3M TIP | 6.800 | 6.800 | 5.000 | 6.200 | 4.200 | 6.800 | 9.400 | 7.200 | 4.800 | 10.700 |
| 3M CANIN | 8.000 | 8.000 | 7.000 | 8.200 | 5.900 | 10.500 | 9.400 | 9.400 | 5.000 | 11.600 |
| USL | 3.400 | 3.400 | 2.000 | 2.400 | 2.800 | 3.700 | 9.400 | 3.800 | 4.400 | 5.600 |
| CON INCI | 18.800 | 19.200 | 17.000 | 18.600 | 18.400 | 20.000 | 25.200 | 20.000 | 17.500 | 27.400 |
| ROST LEN | 6.400 | 17.600 | 16.000 | 17.200 | 17.300 | 18.600 | 23.400 | 19.000 | 16.500 | 25.600 |
| LACR VID | 6.700 | 7.400 | 7.200 | 6.400 | 7.500 | 8.300 | 9.800 | 9.200 | 7.200 | 10.500 |
| INTORB W | 5.000 | 5.000 | 4.600 | 4.800 | 6.800 | 8.000 | 9.400 | 7.200 | 6.100 | 9.700 |
| CON CANI | 12.800 | 12.400 | 11.000 | 12.000 | 5.300 | 6.100 | 8.800 | 5.200 | 4.700 | 9.900 |
| LOWER TR | 17.900 | 17.400 | 16.800 | 17.200 | 12.400 | 13.400 | 17.000 | 13.500 | 11.500 | 18.800 |
| TR CCN H | 1.900 | 1.400 | 1.600 | 1.200 | 7.400 | 8.400 | 10.200 | 9.200 | 1.600 | 11.600 |
| DENTYTHIC | 1.200 | 1.400 | 1.000 | 1.300 | 2.100 | 2.100 | 2.400 | 1.900 | 1.200 | 1.600 |
| MM1 COR | 3.800 | 3.800 | 3.300 | 3.600 | 1.700 | 1.800 | 2.500 | 1.900 | 1.500 | 2.000 |
| MM2 ANG | 3.500 | 3.800 | 3.200 | 3.700 | 3.800 | 4.000 | 5.200 | 4.200 | 3.600 | 5.700 |
| POST ORB | 4.200 | 4.000 | 4.000 | 4.200 | 4.200 | 4.300 | 5.800 | 4.400 | 3.600 | 5.000 |
| ZYGO BR | 11.200 | 11.200 | 10.800 | 11.200 | 12.200 | 13.000 | 15.900 | 12.700 | 12.100 | 17.400 |
| BCASTE BR | 9.600 | 9.400 | 9.000 | 10.000 | 10.300 | 10.700 | 12.500 | 10.000 | 9.400 | 13.400 |
| MCASTOID L | 11.000 | 10.600 | 10.000 | 10.600 | 11.500 | 12.000 | 13.900 | 11.400 | 10.800 | 14.700 |
| PALATE HT | 6.600 | 7.500 | 6.400 | 7.200 | 6.300 | 8.200 | 9.900 | 9.600 | 7.400 | 11.500 |
| BCASTE HT | 6.600 | 6.800 | 6.400 | 7.000 | 6.300 | 7.200 | 9.000 | 8.800 | 6.600 | 8.800 |
| NTR LENG | 7.000 | 7.200 | 6.200 | 6.500 | 6.500 | 7.200 | 9.100 | 7.400 | 6.200 | 10.000 |
| M3 WIDTH | 1.000 | 1.000 | 1.000 | 1.500 | 0.900 | 0.900 | 1.100 | 0.800 | 0.800 | 1.100 |
| M3 CI | 2.400 | 2.600 | 1.700 | 2.800 | 1.700 | 2.900 | 3.400 | 1.800 | 1.600 | 2.300 |

| HEAD 800 | TM MOPSA | TM NANUA | TM NIANG | TM NIVEI | TM SARAA | TM TREVD | TM THERA | XIPHONYC | TR ACETA | TR BECCA |
|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| TAIL | 66.500 | 57.000 | 91.000 | 79.000 | 71.000 | 89.000 | 72.500 | 59.000 | 47.000 | 62.000 |
| EAR | 25.000 | 23.000 | 34.000 | 34.000 | 35.500 | 38.000 | 29.000 | 24.000 | 39.000 | 37.000 |
| HF | 22.500 | 15.000 | 22.000 | 18.000 | 20.000 | 21.000 | 13.500 | 12.000 | 14.500 | 18.000 |
| TIBIA | 10.000 | 7.000 | 13.200 | 9.500 | 10.500 | 11.000 | 6.000 | 7.300 | 10.500 | 6.500 |
| FOREARM | 14.800 | 9.000 | 0.0 | 13.700 | 14.400 | 17.700 | 12.000 | 10.000 | 10.400 | 12.500 |
| 3 META | 43.700 | 29.000 | 52.100 | 46.300 | 41.200 | 33.000 | 37.200 | 28.400 | 38.600 | 34.700 |
| 3M IPHAL | 43.000 | 30.000 | 53.000 | 47.200 | 42.000 | 35.000 | 38.900 | 29.100 | 39.000 | 36.000 |
| 3M 2PHAL | 18.600 | 11.000 | 22.900 | 19.500 | 17.500 | 24.000 | 15.800 | 10.300 | 14.400 | 11.900 |
| 4 META | 41.700 | 21.000 | 21.300 | 18.900 | 14.400 | 23.100 | 12.600 | 9.900 | 12.300 | 11.300 |
| 4M IPHAL | 14.700 | 9.000 | 51.300 | 45.400 | 40.200 | 23.000 | 37.300 | 27.900 | 38.000 | 34.700 |
| 4M 2PHAL | 10.500 | 7.600 | 18.000 | 15.500 | 13.800 | 19.000 | 10.900 | 8.000 | 12.400 | 10.600 |
| 5 META | 27.000 | 20.000 | 31.600 | 29.100 | 24.800 | 32.000 | 25.600 | 19.400 | 29.200 | 25.000 |
| 5M IPHAL | 11.800 | 7.000 | 14.100 | 13.400 | 10.500 | 15.000 | 9.800 | 6.600 | 9.900 | 7.800 |
| 5M 2PTIP | 5.700 | 3.000 | 17.600 | 6.400 | 5.400 | 7.500 | 4.600 | 3.500 | 5.700 | 4.400 |
| 3M TIP | 7.400 | 4.000 | 9.700 | 8.400 | 7.400 | 9.000 | 6.600 | 3.700 | 6.000 | 5.700 |
| 3M CANIN | 3.100 | 3.000 | 9.700 | 8.400 | 7.400 | 9.000 | 6.600 | 3.700 | 6.000 | 5.700 |
| GSN L INCI | 21.200 | 15.000 | 23.000 | 21.000 | 2.900 | 3.000 | 3.400 | 0.0 | 14.600 | 3.700 |
| FOST LEN | 19.600 | 14.000 | 23.000 | 20.000 | 19.300 | 23.000 | 18.800 | 14.900 | 14.100 | 18.400 |
| LACR WID | 8.400 | 5.000 | 9.300 | 8.600 | 8.400 | 9.400 | 7.500 | 6.100 | 6.000 | 8.000 |
| INTORB W | 7.500 | 5.000 | 8.300 | 7.400 | 7.400 | 8.700 | 6.800 | 5.300 | 6.900 | 7.000 |
| CONA CANI | 13.700 | 10.000 | 15.900 | 14.300 | 15.600 | 15.000 | 15.100 | 10.400 | 9.800 | 12.200 |
| LOWER TR | 17.600 | 16.600 | 19.700 | 18.600 | 17.600 | 19.700 | 17.400 | 16.500 | 15.800 | 17.100 |
| TR CON H | 2.000 | 1.600 | 2.500 | 2.200 | 1.900 | 2.000 | 2.500 | 1.500 | 1.700 | 2.500 |
| DENT THIC | 1.800 | 1.000 | 2.400 | 1.900 | 1.800 | 2.000 | 1.800 | 1.100 | 1.000 | 1.500 |
| MON2 COR | 4.200 | 3.000 | 4.900 | 4.400 | 4.000 | 4.000 | 4.000 | 3.100 | 3.300 | 4.500 |
| POST ORB | 4.800 | 3.600 | 4.900 | 4.800 | 4.500 | 5.100 | 4.300 | 3.400 | 3.600 | 3.400 |
| ZYGASE BR | 13.100 | 10.200 | 14.700 | 13.800 | 12.500 | 14.000 | 12.000 | 10.200 | 8.200 | 9.400 |
| 8CASE BR | 11.000 | 8.400 | 11.700 | 10.600 | 10.300 | 12.000 | 9.600 | 9.600 | 8.100 | 11.200 |
| MALOIDB L | 18.100 | 13.600 | 13.600 | 12.500 | 11.700 | 13.000 | 11.200 | 9.600 | 8.600 | 18.100 |
| PALATE L | 7.300 | 5.600 | 7.900 | 6.600 | 6.900 | 8.700 | 6.400 | 5.500 | 5.500 | 6.500 |
| 8CASE HT | 7.300 | 5.600 | 7.900 | 6.600 | 6.900 | 8.700 | 6.400 | 5.500 | 5.500 | 6.500 |
| MTR | 0.800 | 0.700 | 1.200 | 1.000 | 0.700 | 1.000 | 0.800 | 0.600 | 0.900 | 1.100 |
| M3 LENG | 1.800 | 1.600 | 2.300 | 2.000 | 1.800 | 2.300 | 1.600 | 1.500 | 1.600 | 2.400 |
| C1 C1 | 2.800 | 2.100 | 3.100 | 2.100 | 2.600 | 3.300 | 2.600 | 1.800 | 2.200 | 2.400 |

| N3 M3 | TM MOPSA | TM NAKUA | TM NIANG | TM NIVEI | TM SARAA | TM TREVO | TM THERA | XIPHONYC | TR ACETA | TR BECCA |
|-----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| ANT PTER | 6.000 | 4.800 | 6.500 | 6.100 | 6.000 | 6.400 | 5.000 | 4.300 | 3.000 | 4.300 |
| POSTPTER | 2.800 | 2.000 | 2.700 | 2.600 | 2.800 | 2.900 | 2.200 | 1.800 | 1.400 | 1.900 |
| LODCANIN | 2.800 | 2.400 | 2.800 | 3.700 | 2.800 | 3.300 | 2.600 | 2.000 | 1.700 | 2.400 |
| DENT LEN | 14.100 | 10.800 | 16.300 | 14.800 | 13.400 | 16.300 | 13.000 | 10.600 | 2.500 | 3.400 |
| FOR ANT | 12.400 | 19.000 | 16.300 | 12.500 | 11.400 | 13.500 | 11.000 | 10.600 | 10.400 | 13.100 |
| ANGUL L | 3.200 | 2.900 | 3.900 | 3.700 | 3.400 | 4.000 | 3.000 | 2.500 | 2.800 | 11.000 |
| CON CORO | 4.400 | 3.200 | 3.900 | 4.600 | 4.200 | 5.200 | 4.000 | 3.300 | 2.000 | 2.800 |
| CONO MI | 10.800 | 8.000 | 12.000 | 11.200 | 10.200 | 12.200 | 9.700 | 8.100 | 3.000 | 4.400 |
| ANGUL M | 3.200 | 2.900 | 3.900 | 3.900 | 3.400 | 4.000 | 3.600 | 3.000 | 1.800 | 10.000 |
| CORO HT | 4.000 | 2.700 | 4.700 | 4.200 | 3.900 | 4.500 | 3.800 | 3.400 | 1.200 | 2.700 |
| INCI FOR | 3.000 | 2.000 | 2.000 | 2.000 | 2.000 | 2.000 | 2.000 | 2.000 | 4.000 | 4.500 |
| N SHAPE | 6.000 | 5.000 | 4.000 | 5.000 | 6.000 | 4.000 | 4.000 | 5.000 | 1.000 | 1.000 |
| PREMOLAR | 1.000 | 3.000 | 3.000 | 2.000 | 1.000 | 3.000 | 3.000 | 2.000 | 1.000 | 2.000 |
| BASE PIT | 2.000 | 2.000 | 4.000 | 2.000 | 3.000 | 2.000 | 2.000 | 2.000 | 2.000 | 1.000 |
| SAGITT | 2.000 | 2.000 | 2.000 | 2.000 | 3.000 | 2.000 | 2.000 | 2.000 | 1.000 | 1.000 |
| EAR JUNC | 1.000 | 1.000 | 2.000 | 2.000 | 2.000 | 3.000 | 1.000 | 2.000 | 1.000 | 1.000 |
| MI KJES | 2.000 | 3.000 | 3.000 | 2.000 | 3.000 | 3.000 | 2.000 | 2.000 | 2.000 | 1.000 |
| MI KETA | 2.000 | 2.000 | 1.000 | 2.000 | 3.000 | 1.000 | 2.000 | 2.000 | 2.000 | 3.000 |
| GLEND M | 2.400 | 2.900 | 2.700 | 2.600 | 2.200 | 2.800 | 2.200 | 2.100 | 1.200 | 1.700 |
| CONDY L | 1.400 | 2.900 | 2.700 | 2.600 | 2.200 | 2.800 | 2.200 | 2.100 | 1.200 | 1.700 |
| CUP MOL R | 5.600 | 4.000 | 2.600 | 2.000 | 1.600 | 2.500 | 1.600 | 1.400 | 1.100 | 1.500 |
| HA IRYNES | 3.000 | 1.000 | 2.000 | 2.000 | 3.000 | 3.000 | 3.000 | 3.000 | 2.000 | 2.000 |
| LAMBDO | 1.000 | 1.000 | 1.000 | 2.000 | 1.000 | 1.000 | 1.000 | 1.000 | 2.000 | 1.500 |
| LIGIT 3 | 2.000 | 3.000 | 1.000 | 3.000 | 1.000 | 3.000 | 3.000 | 3.000 | 2.000 | 2.000 |
| DIGIT 4 | 5.600 | 3.000 | 1.000 | 2.000 | 3.000 | 1.000 | 3.000 | 3.000 | 2.000 | 2.000 |
| DIGIT 5 | 4.400 | 4.000 | 1.000 | 2.000 | 3.000 | 1.000 | 3.000 | 3.000 | 2.000 | 2.000 |
| ASPET | 2.300 | 3.300 | 4.000 | 3.600 | 4.000 | 4.800 | 4.000 | 4.000 | 4.000 | 3.000 |
| TIP | 2.874 | 2.983 | 2.983 | 2.869 | 3.015 | 2.980 | 2.843 | 2.719 | 4.400 | 2.766 |
| D3 I DS | 1.892 | 6.200 | 6.200 | 1.922 | 6.400 | 6.200 | 1.913 | 6.516 | 6.516 | 1.833 |
| DEARHT | 0.519 | 0.117 | 0.006 | 0.329 | 0.485 | 0.316 | 0.363 | 1.414 | 0.414 | 0.519 |
| CONHT | 0.142 | 0.042 | 0.006 | 0.128 | 0.142 | 0.123 | 0.138 | 0.063 | 0.063 | 0.145 |
| DM1+2 | 0.610 | 0.153 | 0.000 | 0.622 | 0.617 | 0.123 | 0.608 | 0.567 | 0.567 | 0.634 |
| DMH | 0.284 | 0.628 | 0.000 | 0.284 | 0.281 | 0.276 | 0.292 | 0.321 | 0.321 | 0.420 |

| | | | | | | | | | |
|-----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| NEAC BOO | TR JUSUA | TR LORIA | TR MINUA | TR NOREA | TR PHRUO | TR PLANA | C PARVID | C TORCUA | CP BRACA |
| TAIL | 50.500 | 51.000 | 47.500 | 50.500 | 57.000 | 56.500 | 13.000 | 12.000 | 82.500 |
| EAR | 10.000 | 27.000 | 12.700 | 12.100 | 30.000 | 29.000 | 47.000 | 47.700 | 38.500 |
| TRIGIA | 5.800 | 9.000 | 6.300 | 9.400 | 11.000 | 14.400 | 28.500 | 21.000 | 14.600 |
| FORERM | 8.900 | 8.000 | 7.700 | 9.400 | 7.400 | 6.700 | 30.900 | 31.600 | 9.600 |
| 3 MEHA | 36.500 | 30.100 | 30.000 | 30.500 | 35.500 | 35.000 | 80.100 | 75.700 | 43.600 |
| 3M 1PHAL | 12.800 | 12.600 | 11.100 | 12.700 | 37.200 | 35.200 | 80.100 | 75.700 | 48.000 |
| 4M 1PHAL | 10.900 | 12.800 | 10.200 | 12.700 | 12.800 | 12.000 | 38.300 | 41.100 | 21.200 |
| 4M 2PHAL | 36.000 | 32.000 | 29.900 | 35.600 | 36.200 | 34.100 | 78.200 | 76.700 | 18.100 |
| 5M 1PHAL | 11.000 | 10.000 | 10.000 | 10.600 | 10.800 | 10.000 | 37.100 | 36.100 | 18.500 |
| 5M 2PHAL | 7.200 | 7.000 | 6.600 | 7.500 | 4.900 | 4.000 | 23.000 | 23.300 | 5.200 |
| 5M 1TIP | 9.200 | 8.600 | 8.800 | 9.500 | 2.400 | 2.000 | 42.000 | 40.700 | 28.000 |
| 5M 2TIP | 5.200 | 4.000 | 4.000 | 4.400 | 9.300 | 8.100 | 29.800 | 29.500 | 12.800 |
| 5M 1TIP | 5.600 | 5.000 | 4.000 | 4.200 | 4.300 | 4.000 | 15.000 | 14.700 | 6.000 |
| UPL CANIN | 2.300 | 2.000 | 3.000 | 3.400 | 4.300 | 3.000 | 15.000 | 14.500 | 5.200 |
| GSL INCI | 15.100 | 14.000 | 13.400 | 14.900 | 15.200 | 15.200 | 30.600 | 29.500 | 20.400 |
| CONST LEN | 14.500 | 14.000 | 13.400 | 14.900 | 15.200 | 15.200 | 30.600 | 29.500 | 20.400 |
| LACR WID | 6.100 | 5.800 | 5.400 | 6.100 | 6.200 | 6.300 | 12.300 | 12.600 | 8.200 |
| INTORBY | 4.400 | 4.000 | 4.000 | 4.200 | 4.900 | 4.500 | 11.100 | 10.600 | 8.100 |
| CONCANI | 10.000 | 9.000 | 9.000 | 10.200 | 10.500 | 10.200 | 21.700 | 21.400 | 14.100 |
| LOWE TR | 15.900 | 15.000 | 15.200 | 16.000 | 16.200 | 16.000 | 31.000 | 31.000 | 20.000 |
| CONC H | 1.500 | 1.000 | 1.400 | 1.400 | 1.800 | 1.000 | 12.000 | 12.000 | 8.700 |
| DENTITHIC | 1.000 | 1.000 | 1.100 | 1.200 | 1.300 | 1.100 | 3.500 | 3.600 | 2.100 |
| MON1 COR | 3.000 | 3.000 | 2.800 | 3.400 | 3.100 | 3.000 | 7.500 | 7.000 | 4.700 |
| MON2 ANG | 2.700 | 2.500 | 2.400 | 2.800 | 2.700 | 2.500 | 6.100 | 6.000 | 4.000 |
| POST ORB | 3.300 | 3.200 | 3.400 | 3.800 | 3.900 | 3.800 | 9.100 | 9.000 | 5.000 |
| ZYGO BR | 9.300 | 8.000 | 8.200 | 9.600 | 9.800 | 9.700 | 21.000 | 20.500 | 14.400 |
| SCASE BR | 7.800 | 7.000 | 7.000 | 8.400 | 8.000 | 7.700 | 19.500 | 19.500 | 13.500 |
| MASTOIB | 6.500 | 6.000 | 5.900 | 6.600 | 6.000 | 5.000 | 13.000 | 13.500 | 10.800 |
| PALASE LT | 5.200 | 4.400 | 4.800 | 5.000 | 4.800 | 4.500 | 13.000 | 13.500 | 14.400 |
| BCASE LT | 5.800 | 5.000 | 4.800 | 5.400 | 5.700 | 5.400 | 10.600 | 10.600 | 9.000 |
| MTR LENG | 1.100 | 1.000 | 0.800 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 7.000 |
| M3 WIDTH | 1.700 | 1.700 | 1.500 | 1.800 | 1.800 | 1.800 | 2.400 | 2.300 | 1.200 |
| C1 C1 | 2.300 | 2.100 | 1.800 | 2.400 | 2.200 | 2.100 | 4.600 | 4.400 | 2.800 |

| HEAD BOO | CP GREEA | CP PLANA | E AURIPA | E BONARA | E GLAUCA | E HANANA | E MAURUS | E PEROTA | E UNDERA | MP TEMMA |
|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| TAIL | 61.000 | 51.000 | 91.000 | 74.500 | 99.500 | 75.000 | 63.000 | 109.000 | 110.530 | 48.500 |
| EAR | 25.000 | 29.000 | 40.000 | 37.000 | 50.500 | 29.000 | 50.500 | 61.500 | 59.000 | 27.500 |
| HF | 12.500 | 1.000 | 18.200 | 21.000 | 11.800 | 22.500 | 19.000 | 44.000 | 26.000 | 11.000 |
| TIGIA | 9.400 | 5.700 | 12.200 | 8.400 | 12.600 | 8.400 | 9.500 | 13.400 | 14.000 | 5.800 |
| FORARM | 35.000 | 8.100 | 14.800 | 11.800 | 19.000 | 10.200 | 16.700 | 21.500 | 21.300 | 8.400 |
| 3 META | 37.000 | 31.700 | 18.000 | 46.900 | 60.600 | 38.800 | 53.100 | 77.400 | 68.300 | 31.200 |
| 3M 1PHAL | 15.200 | 34.000 | 61.200 | 50.200 | 62.300 | 39.900 | 54.300 | 77.700 | 73.000 | 33.100 |
| 4 META | 13.000 | 14.400 | 26.100 | 20.000 | 25.800 | 15.000 | 23.300 | 31.900 | 32.100 | 11.900 |
| 4M 1PHAL | 35.400 | 12.800 | 24.000 | 17.600 | 24.200 | 16.700 | 21.700 | 29.100 | 29.700 | 14.300 |
| 5 META | 13.400 | 32.800 | 58.400 | 49.000 | 60.200 | 38.000 | 51.700 | 75.600 | 71.200 | 33.000 |
| 4M 2PHAL | 4.200 | 12.200 | 22.300 | 17.600 | 21.600 | 11.200 | 20.400 | 26.400 | 27.000 | 9.800 |
| 5M 1PHAL | 2.1700 | 8.400 | 32.400 | 4.700 | 5.600 | 2.100 | 6.100 | 6.200 | 7.000 | 10.400 |
| 5M 2PTIP | 4.800 | 4.000 | 9.000 | 29.200 | 34.300 | 1.300 | 30.100 | 41.800 | 40.000 | 12.200 |
| 3M TIP | 3.200 | 3.600 | 8.800 | 16.000 | 18.700 | 1.300 | 16.200 | 22.800 | 22.800 | 8.400 |
| UP CANIN | 3.200 | 2.800 | 4.700 | 7.000 | 8.500 | 2.800 | 7.900 | 12.800 | 10.000 | 5.200 |
| GSL INCI | 17.400 | 15.400 | 23.500 | 3.400 | 4.200 | 2.800 | 3.800 | 9.200 | 9.000 | 5.000 |
| CON T LEN | 17.200 | 15.400 | 23.500 | 19.600 | 7.400 | 19.500 | 20.600 | 30.400 | 27.300 | 2.400 |
| ROST WID | 7.000 | 6.000 | 9.200 | 17.800 | 23.300 | 10.500 | 20.100 | 30.600 | 27.000 | 1.200 |
| LN FORB W | 6.000 | 6.000 | 8.800 | 6.800 | 9.600 | 6.200 | 7.900 | 13.000 | 11.000 | 1.500 |
| CON CANI | 15.700 | 15.700 | 16.400 | 5.000 | 6.100 | 4.700 | 6.300 | 9.400 | 9.000 | 2.400 |
| TR ERNTH | 12.100 | 10.800 | 10.100 | 13.600 | 16.800 | 12.900 | 14.600 | 23.400 | 20.400 | 4.800 |
| CON THIC | 1.800 | 1.6500 | 2.300 | 1.700 | 1.0400 | 1.400 | 1.900 | 13.100 | 12.400 | 9.400 |
| DEFT COR | 1.400 | 1.400 | 2.400 | 1.800 | 1.5000 | 1.800 | 1.800 | 2.700 | 2.600 | 2.000 |
| MO21 ANG | 3.100 | 2.800 | 4.900 | 3.800 | 1.400 | 3.800 | 1.300 | 1.800 | 2.500 | 1.200 |
| MO21 ORB | 4.400 | 4.200 | 5.600 | 4.200 | 1.500 | 3.700 | 4.300 | 5.000 | 5.800 | 3.000 |
| ZYDSE BR | 1.600 | 10.400 | 14.600 | 12.800 | 14.400 | 1.100 | 4.000 | 5.000 | 5.800 | 3.000 |
| BCASE BR | 8.000 | 8.000 | 11.400 | 19.800 | 12.600 | 18.700 | 12.400 | 17.800 | 17.500 | 7.000 |
| BCASE IOB | 1.500 | 9.800 | 12.500 | 11.000 | 14.600 | 18.200 | 19.700 | 13.200 | 13.500 | 7.000 |
| MA PLATE L | 1.700 | 6.800 | 10.400 | 8.100 | 9.900 | 16.400 | 10.600 | 15.100 | 11.500 | 8.100 |
| BCASE HT | 6.000 | 5.600 | 7.900 | 7.300 | 9.000 | 6.400 | 8.700 | 19.300 | 19.200 | 4.600 |
| MT R | 0.600 | 0.800 | 9.200 | 1.200 | 8.000 | 7.200 | 7.900 | 1.600 | 1.000 | 5.000 |
| W3 LENG | 1.200 | 1.600 | 2.200 | 1.200 | 12.400 | 1.900 | 0.700 | 2.700 | 2.000 | 1.800 |
| W3 CI | 2.200 | 2.100 | 2.400 | 2.100 | 12.400 | 2.300 | 1.900 | 2.200 | 2.000 | 1.800 |

| | CP | GREEK | PLANA | E | AURIPA | BONARA | E | GLAUCA | E | HANAMA | E | MAURUS | E | PEROTA | E | UNDERA | MP | TENNA |
|------------|----|--------|--------|---|---------|--------|---|---------|---|--------|---|---------|---|---------|---|---------|----|--------|
| M3 | | 4.800 | 4.400 | | 6.400 | 4.900 | | 5.900 | | 4.500 | | 5.400 | | 7.100 | | 7.400 | | 3.600 |
| POSTER | | 1.800 | 1.500 | | 2.400 | 2.100 | | 2.300 | | 2.600 | | 1.900 | | 3.400 | | 3.000 | | 1.400 |
| LOST CANIN | | 2.900 | 2.600 | | 3.100 | 2.800 | | 3.100 | | 2.800 | | 3.000 | | 4.000 | | 3.600 | | 1.800 |
| LENT LEN | | 1.400 | 1.200 | | 1.600 | 1.300 | | 1.700 | | 1.400 | | 1.700 | | 2.200 | | 2.000 | | 2.000 |
| FOR ANT | | 1.700 | 1.500 | | 1.900 | 1.600 | | 1.800 | | 1.500 | | 1.800 | | 2.800 | | 21.000 | | 9.600 |
| ANGUL L | | 2.500 | 2.200 | | 1.400 | 1.100 | | 1.400 | | 1.200 | | 1.300 | | 1.400 | | 18.000 | | 8.100 |
| CONC CO | | 4.500 | 3.500 | | 3.200 | 2.200 | | 3.200 | | 3.200 | | 3.500 | | 4.600 | | 15.000 | | 2.000 |
| CONC MI | | 2.500 | 2.200 | | 1.400 | 1.100 | | 1.200 | | 1.000 | | 1.100 | | 1.900 | | 15.200 | | 3.600 |
| ANGUL M | | 3.200 | 3.400 | | 4.300 | 3.800 | | 4.700 | | 3.600 | | 4.100 | | 5.200 | | 4.600 | | 2.000 |
| INCI FOR | | 1.000 | 1.000 | | 5.300 | 3.800 | | 4.700 | | 3.800 | | 4.100 | | 5.200 | | 6.000 | | 3.000 |
| N SHAF | | 5.000 | 5.000 | | 1.000 | 1.000 | | 1.000 | | 1.000 | | 1.000 | | 1.000 | | 1.000 | | 1.000 |
| PREMO AR | | 1.000 | 1.000 | | 5.000 | 3.000 | | 3.000 | | 3.000 | | 1.000 | | 4.000 | | 4.000 | | 1.000 |
| BA SAGIT | | 1.000 | 1.000 | | 4.000 | 2.000 | | 2.000 | | 5.000 | | 1.000 | | 3.000 | | 3.000 | | 1.000 |
| P SAGIT | | 1.000 | 1.000 | | 3.000 | 1.000 | | 2.000 | | 1.000 | | 2.000 | | 1.000 | | 2.000 | | 1.000 |
| PAR JUNC | | 1.000 | 1.000 | | 2.000 | 2.000 | | 2.000 | | 1.000 | | 2.000 | | 1.000 | | 2.000 | | 2.000 |
| PRINXLES | | 1.000 | 1.000 | | 2.000 | 2.000 | | 2.000 | | 1.000 | | 2.000 | | 4.000 | | 4.000 | | 1.000 |
| MI META | | 1.000 | 1.000 | | 1.000 | 2.000 | | 2.000 | | 3.000 | | 2.000 | | 2.000 | | 1.000 | | 1.000 |
| GLENO L | | 1.800 | 1.600 | | 2.700 | 1.900 | | 2.600 | | 1.800 | | 2.300 | | 3.600 | | 3.200 | | 1.000 |
| GLENO M | | 1.800 | 1.500 | | 3.000 | 2.200 | | 2.700 | | 1.900 | | 1.700 | | 3.200 | | 3.200 | | 1.000 |
| CONDO L | | 1.400 | 1.100 | | 2.000 | 1.600 | | 2.000 | | 1.400 | | 1.700 | | 2.300 | | 2.700 | | 1.000 |
| UP MOL R | | 5.200 | 4.800 | | 6.800 | 5.600 | | 6.700 | | 5.400 | | 6.100 | | 8.500 | | 8.100 | | 4.100 |
| MA TRYMES | | 2.000 | 3.000 | | 2.000 | 2.000 | | 2.000 | | 2.000 | | 2.000 | | 2.000 | | 2.000 | | 3.000 |
| S LAMBO | | 1.000 | 1.000 | | 3.000 | 1.000 | | 3.000 | | 2.000 | | 2.000 | | 2.000 | | 2.000 | | 1.000 |
| DIGIT 3 | | 9.600 | 6.800 | | 120.100 | 94.800 | | 119.900 | | 72.400 | | 125.600 | | 147.900 | | 144.400 | | 63.000 |
| DIGIT 4 | | 52.400 | 49.200 | | 86.700 | 81.300 | | 87.400 | | 54.200 | | 178.200 | | 172.200 | | 106.400 | | 52.000 |
| DIGIT 5 | | 36.700 | 34.100 | | 58.000 | 52.400 | | 61.500 | | 37.000 | | 54.200 | | 77.200 | | 74.000 | | 37.800 |
| SPECT 3 | | 2.856 | 2.630 | | 3.039 | 2.704 | | 2.935 | | 3.035 | | 3.228 | | 2.882 | | 2.674 | | 2.003 |
| TIP FOX | | 6.400 | 6.150 | | 6.430 | 6.000 | | 6.430 | | 6.510 | | 6.540 | | 6.417 | | 6.790 | | 6.700 |
| TP 1 DS | | 1.896 | 1.900 | | 2.049 | 1.809 | | 1.950 | | 1.937 | | 1.948 | | 1.916 | | 1.951 | | 1.877 |
| EXANT I FA | | 0.355 | 0.315 | | 0.314 | 0.448 | | 0.195 | | 0.580 | | 0.358 | | 0.590 | | 0.381 | | 0.353 |
| CONIT DL | | 0.145 | 0.125 | | 0.133 | 0.123 | | 0.087 | | 0.144 | | 0.088 | | 0.079 | | 0.124 | | 0.122 |
| MI+2 DL | | 0.548 | 0.534 | | 0.507 | 0.551 | | 0.595 | | 0.500 | | 0.561 | | 0.548 | | 0.590 | | 0.540 |
| COR H | | 0.315 | 0.304 | | 0.306 | 0.275 | | 0.272 | | 0.264 | | 0.277 | | 0.228 | | 0.286 | | 0.306 |

| HEAD BOO | M | ATERA | M | COI8EA | M | MOLUSS | M | PRITIA | M | SINALA | M | TRINIA | M | MYOP ALB | M | MYOP MHA | M | NEOLATA |
|-----------|---|--------|---|--------|---|--------|---|--------|---|--------|---|--------|---|----------|---|----------|---|---------|
| TAIL | | 86.500 | | 65.000 | | 65.000 | | 79.000 | | 68.000 | | 0.0 | | 86.000 | | 56.000 | | 51.000 |
| EAR | | 43.500 | | 31.500 | | 35.000 | | 38.500 | | 42.000 | | 0.0 | | 41.000 | | 17.000 | | 24.000 |
| HF | | 11.200 | | 12.800 | | 12.100 | | 13.000 | | 12.800 | | 0.0 | | 22.000 | | 13.000 | | 12.300 |
| TIBIA | | 11.200 | | 10.600 | | 19.000 | | 10.400 | | 15.300 | | 8.200 | | 14.000 | | 16.800 | | 5.000 |
| FOHEARM | | 16.400 | | 9.600 | | 13.000 | | 15.400 | | 47.200 | | 15.200 | | 10.000 | | 9.200 | | 8.600 |
| 3 META | | 30.600 | | 33.800 | | 38.000 | | 47.000 | | 44.200 | | 43.600 | | 57.000 | | 34.200 | | 28.600 |
| 3M IPHAL | | 41.100 | | 36.600 | | 39.000 | | 46.600 | | 40.000 | | 45.800 | | 53.700 | | 37.500 | | 30.200 |
| 4 META | | 10.000 | | 16.100 | | 15.000 | | 21.100 | | 21.000 | | 20.000 | | 22.000 | | 13.400 | | 12.000 |
| 4M IPHAL | | 10.000 | | 14.200 | | 18.000 | | 18.400 | | 17.300 | | 17.800 | | 24.000 | | 15.200 | | 9.600 |
| 4M IPHAL | | 30.400 | | 35.600 | | 38.000 | | 45.600 | | 40.300 | | 44.400 | | 16.000 | | 35.200 | | 29.000 |
| 5 META | | 12.800 | | 2.400 | | 3.000 | | 3.000 | | 3.800 | | 4.000 | | 14.700 | | 10.000 | | 10.600 |
| 5M IPHAL | | 20.100 | | 8.900 | | 10.000 | | 27.600 | | 30.400 | | 28.800 | | 35.000 | | 29.400 | | 5.600 |
| 3M TIP | | 9.900 | | 4.200 | | 5.000 | | 1.600 | | 12.000 | | 11.400 | | 15.000 | | 5.200 | | 6.800 |
| UP CANIN | | 5.800 | | 2.800 | | 3.000 | | 4.400 | | 6.800 | | 6.400 | | 8.000 | | 5.000 | | 3.400 |
| GSL INCI | | 3.500 | | 15.000 | | 15.000 | | 3.500 | | 3.500 | | 3.500 | | 4.000 | | 2.500 | | 3.100 |
| ROST LEN | | 17.800 | | 14.900 | | 16.000 | | 20.300 | | 19.200 | | 18.400 | | 23.000 | | 17.300 | | 13.900 |
| ROST WID | | 6.400 | | 5.300 | | 6.000 | | 7.200 | | 6.600 | | 7.000 | | 9.000 | | 6.200 | | 5.700 |
| INTORB W | | 6.000 | | 5.100 | | 5.000 | | 6.500 | | 6.000 | | 6.000 | | 9.000 | | 6.200 | | 6.200 |
| CON CANI | | 15.200 | | 10.700 | | 14.000 | | 15.200 | | 13.000 | | 5.000 | | 16.000 | | 11.500 | | 9.600 |
| LOWE TR | | 17.300 | | 10.900 | | 12.000 | | 14.000 | | 17.500 | | 12.600 | | 17.000 | | 11.000 | | 5.700 |
| TR CON TH | | 1.800 | | 6.400 | | 1.000 | | 8.200 | | 1.500 | | 1.700 | | 19.000 | | 11.000 | | 1.900 |
| DEMT HICR | | 1.800 | | 1.600 | | 1.000 | | 1.800 | | 2.000 | | 1.900 | | 2.000 | | 1.200 | | 1.200 |
| MOH LANG | | 3.800 | | 3.400 | | 3.000 | | 4.000 | | 2.900 | | 3.700 | | 2.500 | | 3.800 | | 3.000 |
| MO2 ORB | | 4.000 | | 3.600 | | 4.000 | | 4.500 | | 4.400 | | 4.200 | | 5.000 | | 2.400 | | 3.400 |
| ZYSC BR | | 4.100 | | 3.800 | | 4.000 | | 4.500 | | 3.800 | | 3.700 | | 5.000 | | 2.400 | | 3.400 |
| POST ORB | | 1.600 | | 10.800 | | 11.000 | | 13.100 | | 9.600 | | 11.400 | | 10.000 | | 1.000 | | 7.000 |
| BUASE BR | | 1.600 | | 8.600 | | 19.000 | | 12.900 | | 11.400 | | 19.000 | | 14.000 | | 9.700 | | 9.300 |
| MASTOIB | | 1.600 | | 10.500 | | 11.000 | | 12.700 | | 7.000 | | 16.700 | | 12.000 | | 9.600 | | 6.800 |
| PLATE L | | 6.200 | | 5.600 | | 6.000 | | 7.700 | | 6.800 | | 7.000 | | 9.700 | | 5.600 | | 4.400 |
| BUASE HT | | 6.300 | | 5.600 | | 6.000 | | 7.700 | | 6.800 | | 7.000 | | 9.700 | | 5.600 | | 4.400 |
| BUAR | | 0.800 | | 0.700 | | 0.000 | | 0.900 | | 0.800 | | 0.800 | | 1.000 | | 0.600 | | 0.900 |
| W3 LENG | | 1.800 | | 1.600 | | 1.000 | | 2.000 | | 2.000 | | 0.800 | | 1.200 | | 1.200 | | 1.600 |
| W3 WIDTH | | 1.200 | | 1.000 | | 1.200 | | 2.000 | | 2.000 | | 0.800 | | 1.200 | | 1.200 | | 1.600 |
| CI C1 | | 2.700 | | 1.300 | | 2.700 | | 2.700 | | 2.700 | | 2.700 | | 2.700 | | 2.700 | | 2.700 |

| HEAD BOB | OTO WARA | OTO PAPU | OTO SECA | OTO WRDA | PLATYMCA | PRO CEN | PRO NASU | SAUROHYS | MIMETILL | NYCTALUS |
|-----------|----------|----------|----------|----------|----------|---------|----------|----------|----------|----------|
| TAIL | 100.000 | 0.0 | 72.000 | 90.000 | 61.000 | 81.500 | 68.000 | 67.000 | 60.000 | 83.000 |
| EAR | 45.000 | 0.0 | 35.500 | 33.000 | 30.500 | 51.000 | 52.000 | 41.000 | 38.000 | 53.000 |
| HF | 12.000 | 20.000 | 9.000 | 12.000 | 17.500 | 15.500 | 13.000 | 17.000 | 13.000 | 17.000 |
| YBIA | 18.600 | 1.600 | 14.000 | 16.100 | 9.300 | 9.600 | 10.000 | 10.300 | 9.600 | 16.700 |
| FOGEARM | 67.200 | 49.400 | 56.800 | 64.400 | 33.000 | 17.600 | 16.300 | 10.300 | 20.500 | 50.500 |
| 3M HETA | 70.200 | 50.800 | 57.400 | 66.500 | 33.700 | 52.600 | 48.000 | 42.400 | 39.500 | 50.400 |
| 3M 1PHAL | 24.200 | 1.800 | 20.300 | 24.600 | 14.200 | 23.000 | 21.800 | 16.200 | 9.000 | 19.300 |
| 4M HETA | 67.000 | 41.200 | 57.000 | 62.000 | 32.000 | 54.200 | 50.000 | 13.600 | 9.000 | 13.300 |
| 4M 1PHAL | 12.000 | 1.700 | 12.900 | 12.600 | 13.000 | 14.200 | 18.000 | 4.000 | 20.500 | 49.600 |
| 5M HETA | 35.400 | 2.500 | 18.600 | 32.700 | 19.600 | 33.500 | 34.000 | 17.100 | 1.600 | 39.900 |
| 5M 1PHAL | 21.800 | 2.300 | 17.800 | 22.000 | 8.800 | 18.200 | 17.200 | 28.100 | 2.500 | 39.400 |
| 3M 2PTP | 15.800 | 1.600 | 9.000 | 9.000 | 8.600 | 18.600 | 13.000 | 17.200 | 1.200 | 5.800 |
| 3M 1TP | 5.800 | 5.000 | 5.600 | 5.000 | 5.800 | 5.600 | 5.000 | 6.700 | 1.600 | 1.900 |
| UD CANIN | 3.800 | 2.800 | 2.900 | 3.200 | 3.400 | 4.000 | 3.200 | 5.700 | 2.500 | 1.500 |
| GUL INCI | 27.200 | 10.700 | 20.300 | 22.000 | 13.500 | 20.000 | 17.200 | 17.600 | 15.100 | 18.500 |
| GRST INCI | 25.200 | 1.800 | 10.300 | 22.000 | 13.500 | 17.400 | 16.500 | 17.800 | 15.100 | 18.500 |
| LNDRB W | 6.000 | 6.000 | 7.800 | 7.000 | 8.500 | 6.600 | 5.800 | 7.500 | 8.200 | 8.500 |
| LNDRB W | 6.000 | 6.000 | 7.800 | 7.000 | 8.500 | 6.600 | 5.800 | 7.500 | 8.200 | 8.500 |
| COLECAN | 18.000 | 1.100 | 12.900 | 15.100 | 9.600 | 13.500 | 17.000 | 12.000 | 10.300 | 17.500 |
| TRK CONH | 10.400 | 1.500 | 7.700 | 9.100 | 1.000 | 6.200 | 1.000 | 1.500 | 5.600 | 2.700 |
| DRK CONH | 1.000 | 1.200 | 0.900 | 1.000 | 1.200 | 1.600 | 1.600 | 1.500 | 1.500 | 4.700 |
| MDY COR | 5.200 | 3.300 | 4.000 | 4.000 | 3.600 | 3.800 | 3.300 | 3.700 | 3.500 | 7.200 |
| MDY COR | 5.200 | 3.300 | 4.000 | 4.000 | 3.600 | 3.800 | 3.300 | 3.700 | 3.500 | 7.200 |
| POST ORB | 4.200 | 1.400 | 4.400 | 5.000 | 3.200 | 4.200 | 10.800 | 1.500 | 1.300 | 13.200 |
| ZVGE BR | 14.200 | 1.500 | 11.200 | 13.000 | 12.600 | 12.600 | 9.400 | 11.500 | 1.300 | 13.200 |
| BUASE BR | 12.200 | 1.400 | 10.200 | 11.600 | 8.200 | 10.200 | 10.400 | 9.200 | 1.300 | 12.600 |
| MA1010B | 13.500 | 1.600 | 1.200 | 12.000 | 10.600 | 1.800 | 10.400 | 1.700 | 1.300 | 9.900 |
| PLATE L | 10.700 | 7.300 | 7.500 | 8.800 | 7.000 | 7.600 | 6.800 | 4.700 | 9.300 | 9.700 |
| BUASE HT | 8.400 | 7.400 | 7.400 | 8.400 | 4.400 | 9.000 | 6.800 | 4.700 | 5.200 | 9.700 |
| MTR | 10.200 | 1.200 | 7.500 | 8.700 | 5.800 | 7.200 | 6.300 | 6.300 | 1.600 | 1.200 |
| W3 LENG | 1.500 | 1.200 | 1.200 | 1.400 | 1.000 | 1.000 | 0.700 | 0.500 | 1.600 | 1.200 |
| W3 WIDTH | 3.000 | 1.800 | 2.400 | 3.000 | 2.500 | 2.200 | 1.900 | 2.000 | 1.500 | 4.300 |
| C1 C1 | 3.000 | 2.000 | 2.400 | 3.000 | 2.500 | 2.200 | 1.900 | 2.000 | 1.500 | 4.300 |

| | OTO MARA | OTO PAPU | OTO SECA | OTO WROA | PLATYNDA | PRO CEN | PRO NASU | SAURDMYS | MIME TILL | NYCTALUS |
|-----------|----------|----------|----------|----------|----------|---------|----------|----------|-----------|----------|
| M3 M3 | 6,100 | 4,400 | 4,600 | 5,700 | 4,000 | 5,600 | 4,900 | 3,900 | 4,200 | 4,900 |
| ANT PTER | 4,000 | 3,000 | 4,400 | 4,000 | 1,900 | 2,800 | 2,300 | 2,900 | 4,200 | 2,700 |
| POSTPTER | 3,000 | 2,400 | 2,800 | 2,900 | 2,400 | 2,500 | 2,300 | 2,200 | 2,200 | 3,000 |
| LD CANIN | 3,000 | 2,700 | 3,000 | 4,000 | 2,100 | 2,600 | 3,000 | 2,000 | 1,100 | 3,000 |
| DENT ANT | 18,000 | 12,000 | 13,000 | 15,600 | 1,900 | 1,600 | 1,600 | 12,400 | 1,100 | 14,600 |
| FOR ANT | 16,000 | 10,900 | 12,000 | 13,900 | 1,900 | 1,600 | 1,700 | 10,400 | 9,000 | 11,600 |
| ANGUL L | 3,000 | 2,600 | 2,900 | 4,600 | 2,600 | 3,400 | 2,900 | 2,800 | 2,700 | 3,300 |
| CON CORO | 13,000 | 8,900 | 9,700 | 11,300 | 2,600 | 3,900 | 3,400 | 2,300 | 2,400 | 4,600 |
| CONO MI | 3,000 | 2,900 | 2,000 | 1,300 | 2,900 | 1,200 | 2,600 | 9,100 | 1,500 | 1,000 |
| ANGUL MT | 3,000 | 2,900 | 2,000 | 3,200 | 4,400 | 3,400 | 3,600 | 1,700 | 1,600 | 4,500 |
| IMCI FOR | 3,000 | 3,000 | 3,000 | 3,000 | 2,000 | 1,000 | 1,000 | 4,400 | 5,000 | 5,000 |
| IN SHAPE | 1,000 | 1,000 | 1,000 | 1,000 | 2,000 | 1,000 | 1,000 | 2,000 | 1,000 | 1,000 |
| PRESOLAR | 1,000 | 1,000 | 1,000 | 1,000 | 2,000 | 1,000 | 1,000 | 2,000 | 1,000 | 1,000 |
| ASAGITT | 2,000 | 3,000 | 1,000 | 5,000 | 1,000 | 2,000 | 2,000 | 2,000 | 1,000 | 1,000 |
| PASAGITT | 2,000 | 3,000 | 1,000 | 1,000 | 1,000 | 2,000 | 2,000 | 2,000 | 1,000 | 1,000 |
| EAR JUNC | 3,000 | 3,000 | 3,000 | 3,000 | 1,000 | 2,000 | 2,000 | 1,000 | 1,000 | 1,000 |
| WRINKLES | 4,000 | 4,000 | 4,000 | 4,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 |
| MI META | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 |
| GLENDO L | 2,000 | 1,700 | 1,600 | 2,000 | 1,400 | 2,000 | 1,700 | 1,000 | 1,300 | 1,000 |
| CONDY L | 1,800 | 1,800 | 1,800 | 2,300 | 1,600 | 2,400 | 2,000 | 1,400 | 1,300 | 1,900 |
| UP MOL R | 1,700 | 1,500 | 1,400 | 1,800 | 1,300 | 1,800 | 1,500 | 1,400 | 1,700 | 2,200 |
| HAIRYNES | 1,000 | 1,000 | 1,000 | 1,000 | 3,000 | 1,600 | 3,000 | 1,400 | 1,400 | 1,700 |
| LAMBDO | 1,000 | 1,000 | 1,000 | 1,000 | 3,000 | 2,000 | 3,000 | 2,000 | 1,000 | 1,000 |
| SIGIT 3 | 126,000 | 91,000 | 103,400 | 121,000 | 66,000 | 1,000 | 1,000 | 2,000 | 3,000 | 2,000 |
| DIGIT 4 | 194,000 | 48,400 | 174,500 | 190,600 | 55,200 | 17,100 | 98,400 | 78,000 | 48,600 | 94,800 |
| DIGIT 5 | 68,000 | 48,700 | 52,500 | 64,200 | 41,000 | 5,800 | 72,000 | 62,000 | 40,300 | 74,000 |
| ASPECT | 2,447 | 2,895 | 2,994 | 2,833 | 2,415 | 2,824 | 2,636 | 46,557 | 32,410 | 55,100 |
| TIP INOX | 65,190 | 64,960 | 64,540 | 65,330 | 66,670 | 6,216 | 67,030 | 66,110 | 62,233 | 65,630 |
| DEAR I FA | 1,159 | 1,881 | 1,933 | 1,899 | 1,610 | 1,895 | 1,767 | 1,042 | 1,500 | 1,721 |
| THIC DL | 0,063 | 0,045 | 0,067 | 0,060 | 0,149 | 0,132 | 0,299 | 0,000 | 0,441 | 0,156 |
| CONC DL | 0,054 | 0,045 | 0,067 | 0,060 | 0,149 | 0,132 | 0,299 | 0,000 | 0,441 | 0,156 |
| MI+2 DL | 0,086 | 0,105 | 0,090 | 0,053 | 0,105 | 0,118 | 0,121 | 0,000 | 0,079 | 0,141 |
| COR H DL | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 | 0,000 |

APPENDIX B

SUMMARY OF NAMES FOR MOLOSSID BATS

(compiled from the literature)

Family **MOLOSSIDAE***Molossi* Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 258.*Molossidae* Gill, 1872, Arrangement of the families of mammals, p. 17 (= *Molossina* Gervais, 1855, Exped. du Comte de Castelnau. Zool., Mamm., p. 52; see Miller, 1907, for additional details).**Allomops** see *Mops***Austronomus** see *Tadarida***Cephalotes** see *Tadarida***Chaerephon** Dobson*Chaerephon* Dobson, 1874, J. Asiatic Soc. Bengal, **43**, pt. 2, p. 144 (subgenus of *Nyctinomus*; type *Nyctinomus johorensis*).*Chaerephon*: Andersen, 1907, Ann. Mus. Civ. Stor. Nat. Genova, ser. 3, **3**, p. 35 (genus).*Lophomops* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 460 (subgenus of *Chaerephon*).*Chaerephon*: Ellerman and Morrison-Scott, 1951, Checklist of Palaearctic and Indian Mammals 1758 to 1946, London, British Museum (Nat. Hist.), p. 135 (subgenus of *Tadarida*).**Chaerephon aloysiisabaudiae** (Festa)*Nyctinomus AloysiiSabaudiae* Festa, 1907, Boll. Mus. Zool. Anat. Comp., **22**, pt. 546, p. 1-2.*Tadarida* (*Chaerephon*) *aloyssiisabaudiae*: Lanza and Harrison, 1963, Z. Säugetierk., **28**, p. 106.*Tadarida cyclotis* Brosset, 1966, Biol. Gabonica, **11**, p. 80.*Tadarida brunnea*: Hayman, Misonne and Verheyen, 1966, Ann. Mus. Roy. African Cent., Ser. Zool. 154, p. 67 (type of *T. brunnea* assigned to *T. aegyptiaca*, Peterson, 1972).**Chaerephon ansorgei** (Thomas)¹*Nyctinomus ansorgei* Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, **11**, p. 318.*Nyctinomus rhodesiae* Roberts, 1946, Ann. Transv. Mus., **20**, p. 307.**Chaerephon bemmelinei** (Jentinck)*Nyctinomus bemmelinei* Jentinck, 1879, Notes Roy. Zool. Mus. Netherlands at Leiden, **1**, p. 125.*Nyctinomus cisturus* Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, **12**, p. 502.¹No previous author has put *ansorgei* into *Chaerephon*, but my analysis supports this change and K. F. Koopman agrees with me.

Chaerephon bivittata (Heuglin)

Nyctinomus bivittatus Heuglin, 1861, Novorum Actorum Acad. Caesareae Leopoldino-Carolinae, **29**, no. 8, pp. 4, 13.

Chaerephon chapini J. A. Allen

Chaerephon (*Lophomops*) *chapini* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 461.

Chaerephon (*Lophomops*) *shortridgei* Thomas, 1926, Proc. Zool. Soc. London, **1926**, p. 289 (valid as a subspecies).

Chaerephon lancasteri Hayman, 1938, Ann. Mag. Nat. Hist. ser. 11, **1**, p. 383 (valid as a subspecies).

Chaerephon gallagheri (Harrison)²

Tadarida (*Chaerephon*) *gallagheri* Harrison, 1975, Mammalia, **39**, p. 313.

Chaerephon jobensis (Miller)

Nyctinomus jobensis Miller, 1902, Proc. Biol. Soc. Washington, **15**, p. 246.

Nyctinomus plicatus colonicus Thomas, 1906, Proc. Zool. Soc. London, **1906**, p. 537 (subspecies is *Chaerephon jobensis colonicus*).

Chaerephon solomonis Troughton, 1931, Proc. Linn. Soc. New South Wales, **56**, p. 207 (valid as a subspecies).

Tadarida jobensis bregullae Felten, 1964, Senckenbergiana Biol., **45**, p. 9.

Chaerephon johorensis (Dobson)

Molossus (*Nyctinomus*) *johorensis* Dobson, 1873, Proc. Asiatic Soc. Bengal, p. 22.

Chaerephon major (Trouessart)

Nyctinomus pumilus var. *major* Trouessart, 1897, Catalogus mammalium tam viventium quam fossilium. 2nd ed. Berlin, **1**, p. 146.

Nyctinomus emini De Winton, 1901, Ann. Mag. Nat. Hist., ser. 7, **7**, p. 40.

Chaerephon (*Lophomops*) *abae* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 464.

Tadarida (*Chaerephon*) *pumila*: Happold, 1967, Sudan Notes Rec., **48**, p. 122 (different from *Dysopes pumilus* Cretzschmar).

Chaerephon nigeriae Thomas

Chaerephon nigeriae Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, **11**, p. 319.

Nyctinomus spillmani Monard, 1933, Bull. Soc. Sci. Nat., Neuchâtel, **57**, p. 51 (valid as a subspecies).

Chaerephon plicata (Buchanan)

Vespertilio plicatus Buchanan, 1800, Trans. Linn. Soc. London, **5**, p. 261, pl. 13.

Nyctinomus bengalensis Desmarest, 1820, Encyclop. Méth. (Mamm.), **1**, p. 116.

Nyctinomus dilatatus Horsfield, 1822, Zool. Res. Java, pl. Java (valid as a subspecies).

Nyctinomus tenuis Horsfield, 1822, Zool. Res. Java, pl. Proewoto (valid as a subspecies).

²Not included in my study.

Dysopes murinus Gray, 1830, Illus. Index Zool., pt. 3, pl. 1.

Chaerephon luzonus Hollister, 1913, Proc. U.S. Nat. Mus., **45**, p. 312 (valid as a subspecies).

Chaerephon plicatus insularis Phillips, 1932, Spolia Zeylan, **16**, p. 334.

Chaerephon plicatus adustus Sody, 1936, Naturk. Tijdschr. Ned.-Ind., **96**, p. 50 (synonym of *C. p. tenuis*).

Chaerephon pumila (Cretzschmar)

Dysopes pumilus Cretzschmar, 1826 [1826–1830], Säugetiere, in Senckenbergische naturforschende Gesellschaft: Atlas zu der Reise in nordlichen Afrika von Eduard Rüppell. Frankfurt am Main, p. 69, pl. 27.

Dysopes limbatus Peters, 1852, Reise nach Mossambique, Säugeth., p. 56, pl. 54 (valid as a subspecies).

Dysopes dubius Peters, 1852, Reise nach Mossambique, Säugeth., p. 60, pl. 15, f. 2 (*C. p. limbatus*?; not of A. Smith, 1833).

Nyctinomus leucogaster A. Grandidier, 1869, Rev. Mag. Zool., ser. 2, **21**, p. 337.

Nyctinomus gambianus De Winton, 1901, Ann. Mag. Nat. Hist., ser. 7, **7**, p. 39.

Nyctinomus pusillus Miller, 1902, Proc. Biol. Soc. Washington, **15**, p. 245.

Nyctinomus hindei Thomas, 1904, Ann. Mag. Nat. Hist., ser. 7, **13**, p. 210 (valid as a subspecies).

Chaerephon websteri Dollman, 1908, Ann. Mag. Nat. Hist., ser. 8, **2**, p. 546 (possibly valid as a subspecies).

Chaerephon pumilus naivashae Hollister, 1916, Smithsonian Misc. Coll., **6**, no. 1, p. 4 (synonym of *C. p. hindei*).

Chaerephon frater J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 456 (possibly valid as a subspecies).

Chaerephon (Lophomops) cristatus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 463.

Chaerophon pumilus elphicki Roberts, 1926, Ann. Transvaal Mus., **11**, p. 245 (valid as a subspecies).

Chaerophon (Lophomops) nigri Hatt, 1928, Bull. Soc. Zool. de France, **53**, p. 374.

Chaerephon (Lophomops) langi Roberts, 1932, Ann. Transvaal Mus., **15**, p. 17 (valid as a subspecies).

Tadarida (Chaerephon) faini Hayman, 1951, Rev. Zool. Bot. Africaines, **45**, p. 82 (possibly valid as a subspecies).

Chaerephon russata J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 458.

Cheiromeles Horsfield

Cheiromeles Horsfield, 1924, Zool. Res. Java, pt. 8.

Chiropetes Gloger, 1841, Gemeinnutziges Hand- u. Hilfsbuch der Naturg., **1**, p. 49.

Cheiromeles parvidens Miller and Hollister

Cheiromeles parvidens Miller and Hollister, 1921, Proc. Biol. Soc. Washington, **34**, p. 100.

Cheiromeles torquatus Horsfield

Cheiromeles torquatus Horsfield, 1824, Zool. Res. Java, pt. 8.

Dysopes cheiropus Temminck, 1826, Monogr. Mammal., **1**, p. 218.

Cheiromeles caudatus Temminck, 1841, Monogr. Mammal., 2, p. 348 (valid as a subspecies).

Cheiromeles jacobsoni Thomas, 1923, Ann. Mag. Nat. Hist., ser. 9, 12, p. 592 (valid as a subspecies).

Cynomops see *Molossops*

Dinops see *Tadarida*

Dysopes see *Tadarida*, *Molossops*, *Eumops*, *Molossus*

Eomops see *Myopterus*

Eumops Miller³

Vespertilio: Shaw, 1800, General Zoology, Mammalia, 1, pt. 1, p. 137 (not Linnaeus, 1758).

Molossus: Schinz, 1821, Das Thierreich, 1, p. 870 (not Geoffroy, 1805).

Dysopes: Wied, 1826, Beitr. Naturg. Brasil., 2, p. 226 (not Illiger, 1811).

Promops: Peters, 1874, Monatsber. K. Preuss. Akad. Wiss. Berlin, 1874, p. 232; Dobson, 1878, Catalog of the Chiroptera in the British Museum, p. 414 (not Gervais, 1855).

Eumops Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85.

Eumops auripendulus (Shaw)

Vespertilio auripendulus Shaw, 1800, General Zoology, Mammalia, 1, pt. 1, p. 137.

Molossus rufus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, 6, p. 155.

Molossus amplexi-caudatus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, 6, p. 156.

Dysopes longimanus Wagner, 1843, Arch. Naturg., 9, pt. 1, p. 367.

Dysopes leucopleura Wagner, 1843, Arch. Naturg., 9, pt. 1, p. 367.

Molossus nasutus: J. A. Allen, 1897, Bull. Amer. Mus. Nat. Hist., 9, p. 115 (not Spix, 1823).

Promops milleri J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., 13, p. 92.

Promops barbatus J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20, p. 228.

Eumops abrasus: Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85 (not Temminck, 1827).

Eumops maurus: Villa-R, 1956, An. Inst. Biol. Mexico, 26, p. 543 (not Thomas, 1901).

Eumops auripendulus: Goodwin, 1960, Amer. Mus. Novitates, 1994, p. 5.

Eumops auripendulus major Eger, 1974, Life Sci. Occas. Pap. Roy. Ontario Mus., 25, p. 2.

Eumops bonariensis (Peters)

Promops bonariensis Peters, 1874, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 232–234.

Molossus bonariensis: Dobson, 1876, Proc. Zool. Soc. London, 1876, p. 715.

³Details in Eger, 1977.

- Promops nanus* Miller, 1900, Ann. Mag. Nat. Hist., ser. 7, 6, p. 470 (valid as a subspecies).
Eumops bonariensis: Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85.
Eumops delticus Thomas, 1923, Ann. Mag. Nat. Hist., ser. 12, 9, p. 341 (valid as a subspecies).
Eumops patagonicus Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, 13, p. 234.
Eumops bonariensis becheri Sanborn, 1932, J. Mammal., 13, p. 355.

***Eumops dabbenei* Thomas⁴**

- Eumops dabbenei* Thomas, 1914, Ann. Mag. Nat. Hist., ser. 8, 13, p. 481.
Eumops perotis dabbenei Sanborn, 1932, J. Mammal., 13, p. 350.

***Eumops glaucinus* (Wagner)**

- Dysopes glaucinus* Wagner, 1843, Arch. Naturg., 9, pt. 1, p. 368.
Molossus ferox Gundlach, 1861, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 149.
Molossus glaucinus: Dobson, 1876, Proc. Zool. Soc. London, 1876, p. 714.
Nyctinomus orthotis H. Allen, 1889, Proc. Amer. Philos. Soc., 26, p. 561.
Promops glaucinus: Miller, 1900, Ann. Mag. Nat. Hist., ser. 7, 6, p. 471.
Eumops glaucinus: Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85.
Molossides floridanus G. M. Allen, 1932, J. Mammal., 13, p. 257 (valid as a subspecies).
Eumops floridanus: Ray, Olsen, and Gut, 1963, J. Mammal., 44, p. 377.

***Eumops hansae* Sanborn**

- Eumops hansae* Sanborn, 1932, J. Mammal., 13, p. 356.
Eumops amazonicus Handley, 1955, Proc. Biol. Soc. Washington, 68, p. 177.

***Eumops maurus* (Thomas)**

- Molossus maurus* Thomas, 1901, Ann. Mag. Nat. Hist., ser. 8, 7, p. 141.
Myopterus maurus: Trouessart, 1904, Cat. Mamm., Suppl., p. 101.
Eumops maurus: Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85.
Eumops geijskesi Husson, 1962, Bats of the Suriname, E. J. Brill, Leiden, p. 246.

***Eumops perotis* (Schinz)**

- Molossus perotis* Schinz, 1821, Das Thierreich, 1, p. 870.
Dysopes perotis: Wied, 1827, Beitr. Naturg. Brasil, 2, p. 227.
Dysopes (Molossus) gigas Peters, 1864, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 381.
Molossus californicus Merriam, 1890, N. Amer. Fauna, 4, p. 31 (valid as a subspecies).
Promops trumbulli Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, 7, p. 190.⁵
Promops perotis: Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, 7, p. 191.
Eumops perotis: Miller, 1906, Proc. Biol. Soc. Washington, 19, p. 85.
Eumops perotis renatae Pirlot, 1965, Nat. Canadien, 92, p. 5.

⁴Not included in my study.

⁵Eger, 1977, considered it a full species, but specimens of *trumbulli* from AMNH which I had in my larger analysis placed so close to *E. perotis* that I did not feel justified in using it in the final analysis. Koopman (1978) considered *trumbulli* a subspecies of *perotis*.

Eumops underwoodi Goodwin

Eumops underwoodi Goodwin, 1940, Amer. Mus. Novitates, **1075**, p. 2.

Eumops sonoriensis Benson, 1947, Proc. Biol. Soc. Washington, **60**, p. 133 (valid as a subspecies).

Eumops underwoodi mederaei Massoia, 1976, Physis, C, **35**, p. 264.

Lophomops see *Chaerephon***Micronomus** see *Mormopterus***Molossops** Peters

Dysopes: Burmeister, 1854, Syst. Uebers. Thiere Brasil, p. 72 (not Illiger, 1811).

Molossops Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575 (subgenus of *Molossus*).

Myopterus Peters, 1869, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 402 (not *Myopterus* Geoffroy, 1813).

Molossops: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 247.

Cynomops Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.

Molossops (Cynomops) brachymeles (Peters)

Molossus (Molossops) brachymeles Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.

Molossus cerastes Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **8**, p. 199 (valid as a subspecies).

Molossops mastivus Thomas, 1911, Ann. Mag. Nat. Hist., ser. 8, **7**, p. 113 (valid as a subspecies).

Molossops brachymeles: Thomas, 1911, Ann. Mag. Nat. Hist., ser. 8, **7**, p. 114.

Cynomops cerastes: Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.

Molossops (Cynomops) brachymeles: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, pp. 118–119.

Molossops (Cynomops) greenhalli (Goodwin)

Cynomops greenhalli Goodwin, 1958, Amer. Mus. Novitates, **1877**, pp. 3–5.

Molossops (Cynomops) planirostris (Peters)

Molossus planirostris Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.

Molossus planirostris paranus Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **8**, p. 190.

Promops nanus Bangs, 1906, Bull. Mus. Comp. Zool., **46**, p. 212 (not Miller, 1900).

Molossops milleri Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**, p. 183 (valid as a subspecies, see Koopman, 1978).

Cynomops planirostris: Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.

Molossops (Cynomops) planirostris: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 119.

Molossops (Molossops) aequatorianus Cabrera⁶

Molossus nasutus Cabrera, 1901, Bol. Soc. Espan. Hist. Nat., **1**, p. 370 (not Spix, 1823).

Molossops aequatorianus Cabrera, 1917, Trab. Mus. Nac. Cienc. Nat., Zool., **31**, p. 20.

Molossops (Molossops) aequatorianus: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 117.

Molossops (Molossops) temminckii (Burmeister)

Dysopes temminckii Burmeister, 1854, Syst. Uebers. Thiere Brasil., p. 72.

Molossus (Molossops) temminckii: Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.

Molossus hirtipes Winge, 1892, E. Mus. Lundii., p. 17.

Molossops temminckii: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 248.

Molossops temminckii sylvia Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, **13**, p. 235.

Molossops temminckii griseiventer Sanborn, 1941, Field Mus. Nat. Hist., Zool. Ser., **27**, p. 385.

Molossops (Molossops) temminckii: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 118.

Molossops (Neoplatymops) mattogrossensis Vieira

Molossops mattogrossensis Vieira, 1942, Arg. Zool. São Paulo, **3**, p. 430.

Molossops temminckii mattogrossensis: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 117.

Cynomops mattogrossensis: Goodwin, 1958, Amer. Mus. Novitates, **1877**, p. 5.

Neoplatymops mattogrossensis: Peterson, 1965, Life Sci. Contrib. Roy. Ontario Mus., **64**, p. 3.

Molossus Geoffroy

Molossus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6**, p. 151.

Dysopes Illiger, 1811, Prodrum systematis mammalium et avium, p. 76.

Molossus ater Geoffroy

Molossus ater Geoffroy, 1805, Bull. Sci. Soc. Philom., **3**, no. 96, p. 279; Ann. Mus. Hist. Nat. Paris, **6**, p. 155.

Molossus castaneus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6**, p. 155.

Molossus ursinus Spix, 1823, Sim. et Vespert. Brasil, p. 59.

Dysopes alecto Temminck, 1827, Monogr. Mammal., **1**, p. 231.

Dysopes holosericeus Wagner, 1843, Arch. Naturg., **9**, pt. 1, p. 368.

Dysopes albus Wagner, 1843, Arch. Naturg., **9**, pt. 1, p. 368.

Molossus myosurus Tschudi, 1844-46, Fauna Peruana, Mamm., p. 83.

Molossus rufus: Dobson, 1876, Proc. Zool. Soc. London, **1876**, p. 710 (not Geoffroy, 1805).

Molossus fluminensis Lataste, 1891, Ann. Mus. Civ. Stor. Nat., Genova, ser. 2, **10**, p. 658.

⁶Not included in my study.

- Molossus nigricans* Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 395 (valid as a subspecies).
Cynomops malagai Villa-R., 1955, Acta Zool. Mexicana, **1**, no. 4, p. 2.

***Molossus bondae* J. A. Allen**

- Molossus bondae* J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20**, p. 228.

***Molossus coibensis* J. A. Allen⁷**

- Molossus coibensis* J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20**, p. 227.

***Molossus macdougalli* Goodwin⁸**

- Molossus pretiosus macdougalli* Goodwin, 1956, Amer. Mus. Novitates, **1757**, p. 3.
Molossus macdougalli Goodwin, 1969, Bull. Amer. Mus. Nat. Hist., **141**, p. 114 (also earlier Goodwin, 1964, Amer. Mus. Novitates, **2195**, p. 20).

***Molossus molossus* (Pallas)**

- V(espertilio) Molossus* (part) Pallas, 1766, Miscellanea zoologica, pp. 45–50.
Vespertilio molossus major Kerr, 1792, Animal Kingdom, p. 97.
Vespertilio molossus minor Kerr, 1792, Animal Kingdom, p. 97.
Molossus obscurus Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.
Molossus longicaudatus Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.
Molossus fusciventer Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.
Molossus crassicaudatus Geoffroy, 1805, Ann. Mag. Hist. Nat. Paris, **6**, p. 156 (valid as a subspecies).
Molossus acuticaudatus Desmarest, 1820, Mammalogie (Brazil), p. 116.
Dysopes velox Temminck, 1827, Monogr. Mammal., **1**, p. 234.
Molossus moxensis D'Orbyigny, 1835, Voy. Amer. Merid., Atlas Zool., lam. **11**, figs. 1–4.
Molossus fuliginosis Gray, 1838, Mag. Zool. and Bot., **2**, p. 501 (not Cooper, 1837).
Molossus tropidorhynchus Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, **4**, p. 6 (possibly valid as a subspecies; K. F. Koopman, *in verbis*).
Dysopes fumarius Schinz, 1844, Syst. Verz. Säug., **1**, p. 114 (not Spix, 1823).
Dysopes olivaceofuscus Wagner, 1850, Abhandl. Bayer. Akad. Wiss., **5**, p. 202.
Dysopes amplexicaudatus Wagner, 1850, Abhandl. Bayer. Akad. Wiss., **5**, p. 202.
M(olossus) aztecus Saussure, 1860, Rev. et. Mag. Zool., Paris, ser. 2, **12**, p. 285 (valid as a subspecies; Gardner, 1966, L. A. County Mus. Nat. Hist. Contrib. in Sci., no. 111, pp. 1–6, reported a full species).

⁷I strongly believe that *M. coibensis* is not a full species. It is more likely a subspecies of *M. molossus* or *M. bondae*. Hall & Kelson (1959) and K. F. Koopman (personal communication) allied *coibensis* with *molossus*, but my analysis places *coibensis* closer to *bondae*.

⁸This taxon was overlooked as a species in my analysis. Hall & Kelson (1959) listed it as a subspecies of *pretiosus*. Specimens of *macdougalli* at AMNH have little development of the sagittal crest. Until a more complete study of the larger forms of *Molossus* is done, I believe I can only report *macdougalli* as it is in the literature right now, i.e., as a full species.

- Molossus pygmaeus* Miller, 1900, Proc. Biol. Soc. Washington, **13**, p. 162 (possibly valid as a subspecies).
Molossus burnesi Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, **15**, p. 584.
Molossus verrilli J. A. Allen, 1908, Bull. Amer. Mus. Nat. Hist., **24**, p. 581 (possibly valid as a subspecies).
Molossus currentium: Miller, 1913, Proc. U.S. Nat. Mus., **46**, p. 89.
Molossus fortis Miller, 1913, Proc. U.S. Nat. Mus., **46**, p. 89 (valid as a subspecies).
Molossus debilis, Miller, 1913, Proc. U.S. Nat. Mus., **46**, p. 90 (valid as a subspecies).
Molossus cherriei J. A. Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35**, p. 529.
Molossus daulensis J. A. Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35**, p. 530 (valid as a subspecies).
Molossus milleri Johnson, 1952, Proc. Biol. Soc. Washington, **65**, p. 197 (possibly valid as a subspecies; K. F. Koopman, *in verbis*).
Molossops planirostris espiritosantensis Ruschi, 1951, Bol. Mus. Biol. Prof. Mello-Leitão Zool., Santa Teresa, Espírito Santo, no. 6, p. 2 (synonymous with *Molossus molossus crassicaudatus*).

Molossus pretiosus Miller

- Molossus pretiosus* Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 396.

Molossus sinaloae J. A. Allen

- Molossus sinaloae* J. A. Allen, 1906, Bull. Amer. Mus. Nat. Hist., **22**, p. 236.

Molossus trinitatus Goodwin⁹

- Molossus trinitatus* Goodwin, 1959, Amer. Mus. Novitates, **1967**, p. 1.

Mops Lesson

- Mops* Lesson, 1842, Nouv. Table. Règne Animal, Mamm., p. 18 (Genotype *Mops indicus* Lesson = *Dysopes mops* F. Cuvier; listed in synonymy of *Nyctinomus* by Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 251; but listed as a genus with distinct characters by Thomas, 1913, J. Bombay Nat. Hist. Soc., **22**, p. 91).
Allomops J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 470 (given as a subgenus of *Mops*).
Philippinopterus Taylor, 1934, Philippine land mammals, p. 314.
Tadarida (*Mops*) Ellerman and Morrison-Scott, 1951, Checklist of Palaearctic and Indian Mammals, 1758 to 1946, p. 133.

Mops brachyptera (Peters)

- Dysopes brachypterus* Peters, 1852, Reise nach Mossambique, Säugeth., p. 59, pl. 15, f. 1.

Mops condylura (A. Smith)

- Nyctinomus condylurus* A. Smith, 1833, South African Quart. J., **1**, p. 54.

⁹Ojasti & Linares (1971) thought *M. trinitatus* was a subspecies of *M. sinaloae*. My analysis shows *trinitatus* to be different from other species of *Molossus* (see text for details).

- Nyctinomus angolensis* Peters, 1870, J. Sci. Math. Phys. Nat. Lisboa, ser. 1, 3, p. 124.
- Mops (Allomops) osborni* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 473 (possibly valid as a subspecies).
- Chaerephon leucostigma* G. M. Allen, 1918, Bull. Mus. Comp. Zool., 61, p. 513.
- Mops angolensis wonderi* Sanborn, 1936, Field Mus. Nat. Hist., Zool. Ser., 20, p. 114 (probably valid as a subspecies).
- Mops osborni occidentalis* Monard, 1939, Archos Mus. Bocage, 10, p. 78.
- Mops osborni fulva* Monard, 1939, Archos Mus. Bocage, 10, p. 78.
- Mops angolensis orientis* G. M. Allen and Loveridge, 1942, Bull. Mus. Comp. Zool., 79, p. 166 (possibly valid as a subspecies).
- Chaerephon emini*: Wroughton, 1911, Ann. Mag. Nat. Hist., ser. 8, 8, p. 458 (specimen from Rosieres [not *Nyctinomus emini* De Winton]).

Mops congica J. A. Allen

- Mops congicus* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 467.

Mops demonstrator (Thomas)

- Nyctinomus demonstrator* Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, 12, p. 504.
- Mops (Allomops) faradjius* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 476.
- Chaerephon emini*: G. M. Allen, 1914, Bull. Mus. Comp. Zool., 54, p. 352 (specimen from Aradeiba [not *Nyctinomus emini* De Winton]).
- Chaerephon bivittatus*: G. M. Allen, 1914, Bull. Mus. Comp. Zool., 54, p. 352 (specimens from El Garef [not *Nyctinomus bivittatus* Heuglin]).

Mops leonis (Thomas)

- Nyctinomus leonis* Thomas, 1908, Ann. Mag. Nat. Hist., ser. 8, 2, p. 373.
- Nyctinomus ochraceus* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 455 (possibly valid as a subspecies).

Mops midas (Sundevall)

- Dysopes midas* Sundevall, 1843, Kgl. Svenska Vetensk. Akad. Handl., p. 207.
- Nyctinomus miarensis* A. Grandidier, 1869, Rev. Mag. Zool., ser. 2, 21, p. 337 (valid as a subspecies).
- Nyctinomus unicolor* A. Grandidier, 1870, Rev. Mag. Zool., ser. 2, 22, p. 44.

Mops mops (de Blainville)

- Dysopes mops* F. Cuvier, 1824, Dents des Mamm., p. 250 (*nomen nudum*).
- Molossus mops* H. D. de Blainville, 1840, Osteogr. Vespertilio, p. 101.
- Mops indicus* Lesson, 1842, Nouv. Tabl. Regn. Anim., p. 18.

Mops nanula J. A. Allen

- Mops (Allomops) nanulus* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 477.
- Mops calabarensis* Hayman, 1940, Trans. Zool. Soc. London, 24, p. 677.

Mops niangarae J. A. Allen

- Mops niangarae* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 468.

Mops niveiventer Cabrera and Ruxton

Mops angolensis niveiventer Cabrera and Ruxton, 1926, Ann. Mag. Nat. Hist., ser. 9, 17, p. 594.

Mops chitauensis Hill, 1937, Amer. Mus. Novitates, 916, pp. 2, 3.

Mops sarasinorum (Meyer)

Nyctinomus sarasinorum Meyer, 1899, Abhandl. Zool. Anthropol.-Ethn. Mus. Dresden, ser. 7, 7, p. 15, pls. 4, 10, 11.

Philippinopterus lanei Taylor, 1934, Philippine Land Mammals, p. 314 (Hill, 1961, listed it as a distinct species; I list it as a subspecies because it shows little difference from *M. sarasinorum* in a large preliminary study).

Mops spurrelli (Dollman)¹⁰

Xiphonycteris spurrelli Dollman, 1911, Ann. Mag. Nat. Hist., ser. 8, 7, pp. 210, 211.

Mops thersites (Thomas)

Nyctinomus thersites Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, 12, p. 634.

Mops (Allomops) occipitalis J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 474.

Mops trevori J. A. Allen

Mops trevori J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., 37, p. 469.

Mormopterus Peters

Mormopterus Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 258 (subgenus of *Nyctinomus*).

Mormopterus: Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 253 (listed only New World forms in the genus and included *M. norfolkensis* as a species of *Nyctinomus*).

Micronomus: Troughton, 1943, Furred animals of Australia, 2nd ed., p. 364 (listed earlier in Iredale & Troughton, 1934; includes only Australian forms).

Mormopterus (Mormopterus) acetabulosus (Hermann)

Vespertilio acetabulosus Hermann, 1804, Observationes Zoologicae, p. 19.

Dysopes natalensis A. Smith, 1847, Illustr. Zool. S. Africa, Mamm., pl. 49 and text (valid as a subspecies).

Mormopterus acetabulosus Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 254.

Mormopterus (Mormopterus) beccarii Peters

Mormopterus beccarii Peters, 1881, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 484.

Nyctinomus astrolabiensis Meyer, 1899, Abhandl. Zool. Anthropol.-Ethn. Mus. Dresden, ser. 7, 7, p. 19 (valid as a subspecies).

¹⁰Probably an intensive study of males and females of both *M. spurrelli* and *M. nanula* should be done to see if these are actually one species.

Mormopterus (Mormopterus) doriae Andersen¹¹

Mormopterus doriae Andersen, 1907, Ann. Mus. Civ. Stor. Nat. Genova, **3**, p. 38.

Mormopterus (Mormopterus) jugularis (Peters)

Nyctinomus (Mormopterus) jugularis Peters, 1865, in Sclater, Proc. Zool. Soc. London, **1865**, p. 468.

Nyctinomus albiventer Dobson, 1877, Proc. Zool. Soc. London, **1876**, p. 733.

Mormopterus (Mormopterus) kalinowskii (Thomas)

Nyctinomus kalinowskii Thomas, 1893, Proc. Zool. Soc. London, **1893**, p. 334.

Mormopterus kalinowskii: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 254.

Mormopterus (Mormopterus) loriae (Thomas)

Nyctinomus loriae Thomas, 1897, Ann. Mus. Civ. Stor. Nat. Genova, **18**, p. 609.

Tadarida loriae cobourgiana Johnson, 1959, Proc. Biol. Soc. Washington, **72**, p. 185.

Tadarida loriae ridei Felten, 1964, Senckenbergiana Biol., **45**, p. 6.

Mormopterus (Mormopterus) minutus (Miller)

Nyctinomus minutus Miller, 1899, Bull. Amer. Mus. Nat. Hist., **12**, p. 173.

Mormopterus minutus: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 254.

Mormopterus (Mormopterus) norfolkensis (Gray)

Molossus norfolkensis Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, **4**, p. 7.

Mormopterus (Mormopterus) phrudus (Handley)

Mormopterus phrudus Handley, 1956, Proc. Biol. Soc. Washington, **69**, p. 197.

Mormopterus (Mormopterus) planiceps (Peters)

Nyctinomus planiceps Peters, 1866, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 23.

Molossus wilcoxi Kreffft, 1871, Austr. Vertebrata, fossil and recent, p. 4 (*nomen nudum*).

Nyctinomus petersi Leche, 1844, Proc. Zool. Soc. London, **1844**, p. 49.

Mormopterus (Platymops) setiger Peters

Mormopterus setiger Peters, 1878, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 196.

Platymops macmillani Thomas, 1906, Ann. Mag. Nat. Hist., ser. 7, **17**, p. 499 (valid as a subspecies).

Platymops barbatogularis Harrison, 1956, Ann. Mag. Nat. Hist., ser. 12, **9**, p. 549.

Platymops setiger: Harrison and Fleetwood, 1960, Durban Mus. Novitates, **15**, pp. 277–278.

Mormopterus (Sauromys) petrophilus (Roberts)

Platymops (Sauromys) petrophilus Roberts, 1917, Ann. Transvaal Mus., **6**, p. 4.

¹¹Not included in my study.

- Platymops (Sauromys) haagneri* Roberts, 1917, Ann. Transvaal Mus., 5, p. 5 (valid as a subspecies).
Platymops (Sauromys) haagneri umbratus Shortridge and Carter, 1938, Ann. S. African Mus., 32, p. 282 (valid as a subspecies).
Platymops petrophilus erongensis Roberts, 1946, Ann. Transvaal Mus., 20, p. 308.
Platymops petrophilus fitzsimonsi Roberts, 1946, Ann. Transvaal Mus., 20, p. 308.
Sauromys petrophilus: Peterson, 1965, Life Sci. Contrib. Roy. Ontario Mus., 64, p. 12.

Myopterus Geoffroy

- Myopterus*: Geoffroy, 1818, Description de l'Égypte, Paris, 2, p. 113.
Eomops Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, 16, p. 572.

Myopterus albus Thomas

- Myopterus senegalensis* Oken, 1816, Lehrbuch der Naturg., 3, p. 933 (original type specimen lost; name invalid).
Myopteris daubentonii Desmarest, 1820, Encyclopédie Méthodique Mammalogie, 1, p. 132 (type specimen lost; Hill, 1969, suggested *incertae sedis*; Hayman & Hill, 1971, suspected synonymous with *albus*).
Myopterus albus Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, 16, p. 469.

Myopterus whitleyi (Scharff)

- Mormopterus whitleyi* Scharff, 1900, Ann. Mag. Nat. Hist., ser. 7, 6, p. 569.
Eomops whitleyi: Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, 16, p. 572.

Nyctinomops Miller

- Nyctinomops* Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393.
Tadarida: Shamel, 1931, Proc. U.S. Nat. Mus., 78, p. 1 (part, *macrotis* group).

Nyctinomops aurispinosa (Peale)

- Dysopes aurispinosus* Peale, 1848, U.S. Expl. Exp., 8, Mammalogy and Ornithology, p. 21 (Ed. 1).
Molossus aurispinosus: Cassin, 1858, U.S. Expl. Exp., 8, Mammalogy and Ornithology, pp. 5-7 (Ed. 2).
Nyctinomops aurispinosus: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393.
Tadarida aurispinosa: Shamel, 1931, Proc. U.S. Nat. Mus., 78, p. 11.
Tadarida similis Sanborn, 1941, Field Mus. Nat. Hist., Zool. Ser., 27, p. 386.

Nyctinomops femorosacca (Merriam)

- Nyctinomops femorosaccus* Merriam, 1889, N. Amer. Fauna, no. 2, p. 23.
Nyctinomops femorosaccus: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393.
Tadarida femorosacca: Miller, 1924, Bull. U.S. Nat. Mus., 128, p. 86.

Nyctinomops laticaudata (Geoffroy)

- Molossus laticaudatus* Geoffroy, 1805, Ann. Mus. Paris, 6, p. 156.
Molossus caecus Rengger, 1830, Säugethiere Paraguay, p. 88.

- Nyctinomus gracilis* Dobson, 1876, Proc. Zool. Soc. London, 1876, p. 731.
Nyctinomus europus H. Allen, 1889, Proc. Amer. Philos. Soc., 26, pp. 558–561.
Nyctinomops yucatanicus Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393 (valid as a subspecies).
Nyctinomops laticaudata: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393.
Tadarida laticaudata: Shamel, 1931, Proc. U.S. Nat. Mus., 78, p. 12.
Tadarida laticaudata ferruginea Goodwin, 1954, Amer. Mus. Novitates, 1607, p. 2.
Tadarida laticaudata macarenensis Barriga-Bonilla, 1965, Caldasia (Colombia), 9, p. 249.

***Nyctinomops macrotis* (Gray)**

- V(espertilio) Molossus* (part) Pallas, 1766, Miscellanea Zoologica, pp. 49–50.
Nyctinomus macrotis Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, 4, p. 5.
Dysopes auritus Wagner, 1843, Arch. Naturg., 9, pt. 1, p. 368.
Nyctinomus megalotis Dobson, 1876, Proc. Zool. Soc. London, 1876, p. 728.
Nyctinomus depressus Ward, 1891, Amer. Nat., 23, p. 747.
Promops affinis J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., 13, p. 91.
Promops depressus: J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., 13, p. 91.
Nyctinomops macrotis: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54, p. 393.
Nyctinomus nevadensis Miller, 1902, Proc. Biol. Soc. Washington, 15, p. 250.
Nyctinomus molossus: Miller, 1913, Proc. U.S. Nat. Mus., 46, p. 86 (footnote 4).
Nyctinomus aequatorialis J. A. Allen, 1914, Bull. Amer. Mus. Nat. Hist., 33, p. 386.
Tadarida molossa: Hershkovitz, 1949, Proc. U.S. Nat. Mus., 99, p. 452.
Tadarida macrotis: Husson, 1962, The bats of the Suriname, E. J. Brill, Leiden, pp. 256–259.

***Otomops* Thomas**

- Otomops* Thomas, 1913, J. Bombay Nat. Hist. Soc., 22, p. 90.

***Otomops formosus* Chasen¹²**

- Otomops formosus* Chasen, 1939, Treubia, 17, p. 186.

***Otomops martiensseni* (Matschie)**

- Nyctinomus martiensseni* Matschie, 1897, Arch. Naturg., 63, pt. 1, p. 84.
Otomops icarus Chubb, 1917, Ann. Durban Mus., 1, p. 433 (valid as a subspecies).
Otomops madagascarensis Dorst, 1953, Mem. Inst. Sci. Madagascar, ser. A, 8, p. 236 (valid as a subspecies; Valdivieso et al., 1979, listed it as a distinct species).

***Otomops papuensis* Lawrence**

- Otomops papuensis* Lawrence, 1948, J. Mamm., 29, p. 413.

¹²Not included in my study.

Otomops secundus Hayman

Otomops secundus Hayman, 1952, Bull. Brit. Mus. (Nat. Hist.), Zool., 1, p. 314.

Otomops wroughtoni

Otomops wroughtoni Thomas, 1913, J. Bombay Nat. Hist. Soc., 22, p. 91.

Philippinopterus see *Mops***Platymops** see *Mormopterus***Promops** Gervais

Promops Gervais, 1855, Mammifères, in Castelnau, Exped. dans les parties centrales de l'Amer. du Sud. . . . pt. 7, p. 58. (Type *Promops ursinus* Gervais = *Molossus nasutus* Spix.)

Promops centralis Thomas

Promops centralis Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, 16, p. 62.

Promops occultus Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, 16, p. 62 (valid as a subspecies).

Promops davisoni Thomas, 1921, Ann. Mag. Nat. Hist., ser. 8, 8, p. 139 (valid as a subspecies).¹³

Promops nasutus (Spix)

Molossus nasutus Spix, 1823, Sim. Vespert. Brasil., p. 59.

Molossus fumarius Spix, 1823, Sim. Vespert. Brasil., p. 60.

Dysopes rufocastaneus Schinz, 1844, Syst. Verz. Säug., 1, 142.

Promops ursinus Gervais, 1855, Mammifères, in Castelnau, Exped. dans les parties centrales de l'Amer. du Sud. . . . pt. 7, p. 59.

Promops fosteri Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 259.

Promops nasutus: Miller, 1907, Bull. U.S. Nat. Mus., 57, p. 260.

Promops pamana Miller, 1913, Proc. Biol. Soc. Washington, 26, p. 33.

Promops ancilla Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, 16, p. 63 (valid as a subspecies).

Promops nasutus downsi Goodwin, 1962, Amer. Mus. Novitates, 2080, p. 10 (possibly valid as a subspecies).

Sauromys see *Mormopterus***Tadarida** Rafinesque

Tadarida Rafinesque, 1814, Précis des découvertes et travaux somiologiques. . . . , p. 55 (Type, *Cephalotes teniotes* Rafinesque).

Nyctinomus E. Geoffroy, 1818, Description de l'Égypte, 2, p. 114 (Type, *Nyctinomus aegyptiacus* E. Geoffroy).

¹³Ojasti & Linares (1971) thought that *P. davisoni* was a subspecies of *P. centralis*. Koopman (1978) agreed, but did not mention comparing *davisoni* with *nasutus*. Specimens of *davisoni* from AMNH which I measured were more similar to *nasutus* than to *centralis* in my large preliminary study, which is why I list *davisoni* with *nasutus* in specimens examined. Both are of similar small size, with *centralis* being the larger.

Nyctinoma Bowdich, 1821, Anal. Nat. Class. Mamm., p. 288.

Nyctinomes Gray, 1821, London Med. Repos., **15**, p. 299.

Nyctinomia Fleming, 1822, Philos. Zool., **2**, p. 178.

Dinops Savi, 1825, N. Gior. Lett. Pisa, Sci., **10**, p. 229 (*Dinops cestoni* Savi = *Cephalotes teniotis* Rafinesque).

Dysopes: Cretzschmar, 1830 or 1831, in Ruppell, Atlas zu der Reise im nördlichen Afrika, Säugethiere, p. 69 (not of Illiger, 1811).

Austronomus Iredale and Troughton, 1934, Mem. Austral. Mus., **6**, p. 100 (*nomen nudum*; later validated by Troughton, 1941, Furred animals of Australia, ed. 1, p. 360).

***Tadarida aegyptiaca* (E. Geoffroy)**

Nyctinomus aegyptiacus E. Geoffroy, 1818, Description de l'Egypte, **2**, p. 128, pl. 2, no. 2.

Dysopes geoffroyi Temmink, 1827, Monogr. Mammal., **1**, p. 226.

Nyctinomus tragatus Dobson, 1874, J. Asiatic Soc. Bengal, **43**, ser. 2, p. 143.

Dysopes talpinus Heuglin, 1877, Reise in Nordost-Afrika. Braunschweig, vol. 2, p. 28.

Nyctinomus anchietae Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 82.

Nyctinomus brunneus Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 83.

Nyctinomus bocagei Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 84 (valid as a subspecies).

Nyctinomus tongaensis Wettstein, 1916, Anz. K. Akad. Wiss. Wien, **53**, p. 192.

Tadarida sindica Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, p. 732 (valid as a subspecies).

Tadarida thomasi Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, p. 732 (valid as a subspecies).

Tadarida gossei Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, pp. 732–733 (valid as a subspecies).

***Tadarida africana* (Dobson)¹⁴**

Nyctinomus africanus Dobson, 1876, Ann. Mag. Nat. Hist., ser. 4, **17**, p. 348.

***Tadarida australis* (Gray)**

Molossus australis Gray, 1838, Mag. Zool. Bot., **2**, p. 501.

Nyctinomus albidus Leche, 1884, Proc. Zool. Soc. London, **1884**, p. 58, fig. 3.

Nyctinomus australis atratus Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, **14**, p. 456.

Austronomus australis: Troughton, 1941, Furred Animals of Australia, ed. 1, p. 360.

***Tadarida brasiliensis* (I. Geof. St.-Hilaire)**

Nyctinomus brasiliensis I. Geoffroy St.-Hilaire, 1824, Ann. Sci. Nat., **1**, p. 343.

Dysopes nasutus Temminck, 1827, Monogr. Mammal., **1**, p. 233.

¹⁴According to Dieter Kock (1975, Stuttgarter Beiträge zur Naturkunde, ser. A. (Biol.), no. 272, pp. 1–9), the earliest name for *africana* was *Nyctinomus* (*Dysopes*) *ventralis* Heuglin, 1861, Nov. Act. Acad. Caes. Leop.-Carol., **29**, pp. 4, 11. This name came to my attention only recently.

- Nyctinomus murinus* Gray, 1827, Cuvier's Animal Kingdom, Griffith ed., 5, p. 66 (valid as a subspecies).
- Nyct(icea) cynocephala* LeConte, 1831, Cuvier's Animal Kingdom, McMurtie's edition, 1, p. 432 (valid as a subspecies).
- Molossus fuliginosus* Cooper, 1837, Ann. Lyc. Nat. Hist. New York, 4, p. 67.
- Dysopes naso* Wagner, 1840, in Schreber, Die Säugethiere, Suppl., 1, p. 475.
- Rhinopoma carolinensis* Gundlach (not Geoffroy), 1840, Wiegmann Archiv., 1, p. 358.
- Molossus mexicanus* Saussure, 1860, Rev. Mag. Zool., Paris, ser. 2, 12, p. 283 (valid as a subspecies).
- Nyctinomus musculus* Gundlach, 1861, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 149 (valid as a subspecies).
- Nyctinomus mohavensis* Merriam, 1889, N. Amer. Fauna, no. 2, p. 25.
- Nyctinomus antillarum* Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, p. 398 (valid as a subspecies).
- Nyctinomus bahamensis* Rehn, 1902, Proc. Acad. Nat. Sci. Philadelphia, p. 641 (valid as a subspecies).
- Mormopterus peruanus* J. A. Allen, 1914, Bull. Amer. Mus. Nat. Hist., 33, p. 311.
- Tadarida intermedia* Shamel, 1931, Proc. U.S. Nat. Mus., 78, p. 7 (valid as a subspecies).
- Tadarida constanzae* Shamel, 1931, Proc. U.S. Nat. Mus., 78, p. 10 (valid as a subspecies).
- Tadarida texana* Stager, 1942, Bull. Southern California Acad. Sci., 41, p. 49.

***Tadarida espiritosantensis* (Ruschi)¹⁵**

- Tadarida espiritosantensis* Ruschi, 1951, Bol. Mus. Biol. Prof. Mello-Leitão Zool., Santa Teresa, Espírito Santo, no. 7, p. 19.

***Tadarida fulminans* (Thomas)**

- Nyctinomus fulminans* Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, 12, p. 501.
- Tadarida mastersoni* Roberts, 1946, Ann. Transvaal Mus., 20, p. 306.

***Tadarida kuboriensis* McKean and Calaby¹⁶**

- Tadarida kuboriensis* McKean and Calaby, 1968, Mammalia, 32, p. 375.

***Tadarida lobata* (Thomas)**

- Nyctinomus lobatus* Thomas, 1891, Ann. Mag. Nat. Hist., ser. 6, 7, p. 303.

***Tadarida teniotis* (Rafinesque)**

- Cephalotes teniotis* Rafinesque, 1814, Précis. Découv. Somiol., p. 12.
- Dinops cestoni* Savi, 1825, N. Giorn. Lett. Pisa, Sci., 10, p. 235.
- Dysopes rupelii* (sic) Temminck, 1826, Monogr. Mammal., 1, p. 224, pl. 18 (valid as a subspecies).
- Dysopes savii* Schinz, 1840, European Fauna, 1, p. 5.
- Nyctinomus insignis* Blyth, 1861, J. Asiatic Soc. Bengal, 30, p. 90 (valid as a subspecies).

¹⁵Mentioned in Pine & Ruschi, 1976, An. Inst. Biol. Univ. Autón. Mexico, 47, ser. Zool., pp. 183–196; not included in my study.

¹⁶This may eventually prove to be a subspecies of *T. australis*.

- Nyctinomus taeniotis* Thomas, 1891, Proc. Zool. Soc. London, 1891, p. 182.
Dysopes midas: Schulze, 1897, Helios, Berlin, 14, p. 95 (not of Sundevall, 1842).
Tadarida latouchei Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, 5, p. 283.
Tadarida septentrionalis Kishida and Mori, 1931, Zool. Mag. Tokyo, 43, p. 379
 (nomen nudum).

Vespertilio see *Eumops*

Xiphonycteris see *Mops*

APPENDIX C

KEY TO GENERA AND SUBGENERA OF MOLOSSID BATS

- 1a. Ears usually widely separated, basisphenoid pits usually shallow or nonexistent (*Myopterus* an exception).
 - 2a. Palate without anterior emargination, no wrinkles on lips.
 - 3a. Tooth number 26 (1/1, 1/1, 1/2, 3/3), M³ V-shaped, 2nd phalanx of digit IV from 16–20 per cent of total length of digit IV.
 - 4a. Body size very large (FA around 75 mm, GSL near 30 mm), hair short and sparse to the point of being naked *Cheiromeles*
 - 4b. Body size smaller.
 - 5a. Basisphenoid pits very deep (distinct hole 1+mm in depth) *Myopterus*
 - 5b. Basisphenoid pits shallow, slight cusp on M³, size very small (GSL near 13 mm). . . *Molossops* (*Molossops*)
 - 3b. Tooth number 28 or 30, M³ either V- or N-shaped, 2nd phalanx variable.
 - 6a. Tooth formula 1/2(1), 1/1, 1/2, 3/3 = 28 (26 possibly), 2nd phalanx of digit IV near 7.5 per cent (6.9–8.5) of digit IV, M³ V-shaped *Molossops* (*Cynomops*)
 - 6b. Tooth formula 1/2, 1/1, 2/2, 3/3 = 30, 2nd phalanx of digit IV near 12 per cent of digit IV, M³ N-shaped *Molossops* (*Neoplatymops*)
- 2b. Palate notched anteriorly, coronoid process usually high and curved posteriorly, lips not wrinkled or slightly wrinkled or covered with spines.
 - 7a. Skull not extremely flattened, 28–30 teeth, M³ complete N-shape.
 - 8a. Tooth formula 1/2, 1/1, 1/2, 3/3 . . . New World *Mormopterus*
 - 8b. Tooth formula 1/3, 1/1, 1/2, 3/3 or 1/2, 1/1, 2/2, 3/3 Old World *Mormopterus*
 - 7b. Skull extremely flattened.
 - 9a. PM³ absent, extreme development of lacrimal process, lips covered with thick, spiny hairs . . *Mormopterus* (*Platymops*)
 - 9b. PM³ present (ears not widely separated but meeting in a V) *Mormopterus* (*Sauromys*)
- 1b. Ears not widely separated but just joining to form a V-shaped valley or well-joined over the nose by a band; basisphenoid pits usually medium deep to very deep.

- 10a. No anterior emargination of palate.
 - 11a. Lips unwrinkled, M³ V-shaped.
 - 12a. PM³ absent *Molossus*
 - 12b. PM³ vestigial, domed-palate *Promops*
 - 11b. Lips skirt-like with many fine wrinkles, PM³ present, ears often large and forward facing, M³ variable but usually always with posterior commissure *Eumops*
- 10b. Anterior emargination of palate either slight or deep, lips either deeply wrinkled or skirt-like.
 - 12a. 2nd phalanx of digit IV 9 per cent or greater of digit IV length.
 - 13a. M³ V-shaped or with slight posterior cusp (less than half of length of 2nd cusp), PM³ moderately developed, vestigial or absent, dentary relatively thick (lateral thickness at M₁ 11–15 per cent of dentary length), 4 or 2 lower incisors *Mops*
 - 13b. M³ not always fully developed N-shape but posterior cusp greater than half of length of 2nd cusp, palatal emargination usually slight, relative thickness of dentary rarely over 11 per cent (*Chaerephon jobensis* from Indo-Australian region an exception with about 14 per cent), 2nd phalanx of digit IV around 14–17 per cent *Chaerephon*
 - 13c. M³ usually well-developed N-shape, deeply notched anterior palate, PM³ usually well developed, 2nd phalanx of digit IV usually 9–12 per cent of digit IV (the Australian *Tadarida australis* and New Guinean *T. kuboriensis* are exceptions at 17 per cent of digit IV) *Tadarida*
 - 14. If basisphenoid extremely deep *Otomops*
 - 15. If skull extremely flattened ... *Mormopterus (Sauromys)*
 - 12b. 2nd phalanx between 3 and 5 per cent of digit IV, narrow rostrum and deeply notched anterior palate *Nyctinomops*

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